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13.

The Behavior of Two Captive Specimens of the Lowland Gorilla, *Gorilla gorilla gorilla* (Savage & Wyman).[1]

B. F. Riess,[2] Sherman Ross,[3] S. B. Lyerly,[4] and H. G. Birch.[5]

Behavior Research Fellows (1948), *New York Zoological Society.*

(Plates I & II; Text-figures 1 & 2).

I. Introduction.

The field of comparative behavior research has long been subject to two methodological factors which have to a certain extent prevented the attainment of its goal, namely the securing of information on behavioral processes of representative species of a wide range of living organisms. The first factor has been the concentration of research workers on those animals which are adaptable to the limited conditions of laboratories. This emphasis on a few selected species has led to the second factor, the acceptance of the conventional laboratory as the prototype of habitat for the species under investigation. Both these methodological limitations have arisen in part from the same set of circumstances, the relative lack of availability of less adaptable organisms and the expense of field studies. The increasing number of investigations under naturalistic field conditions and of studies on rare specimens under favorable conditions has provided additional evidence of the fruitfulness of the extension of both laboratory and field methodology to specimens other than those generally used in comparative behavior laboratories.

It is one of the purposes of this paper to point to a source of data which can facilitate not only the collection of more information on a wider variety of animals but which can also serve as a training facility for field-workers and others. Within the reach of researchers in most large cities there exist collections of living animals in great variety of species and under varied living conditions. The reference is to the zoological parks and exhibition areas. In many of these, natural habitat conditions are approximated and even the differences can be fertile sources of comparative psycho-ecological studies.

In 1937, Carpenter (2) published a study of two young male mountain gorillas, *Gorilla gorilla berengei,* resident at the San Diego Zoo. In this paper he pointed to the opportunities presented by the fourteen specimens of the largest of the great apes which he listed as available in the zoological parks of the world. Gorillas offer a dramatic field for this type of research since they are, with the exception of the orang-utan, the least studied of the anthropoid apes. The present paper seeks to compare Carpenter's data with those obtained in a study of male and female pre-adolescent lowland gorillas, *Gorilla gorilla gorilla,* in the New York Zoological Park (Bronx Zoo). Such comparative data as can be assembled will be helpful to workers who seek a base line for similar investigation elsewhere. That these investigations are possible is demonstrated in Table I which lists the location and over-all biological indices of the specimens now resident in various collections. The number of gorillas in the United States is increasing. In 1937 there were only eight specimens in this country; today there are twenty-four.

Other than Carpenter's study, material on the behavior of the gorilla is found only in a limited number of papers. Yerkes' pioneer work (6) with the pre-adolescent female mountain gorilla, Congo, is known to all students of comparative psychology. Bingham's 1932 observations (1) on gorillas in their native habitat and Valker's similar study in the Gaboons (5) in 1931 are the only other relevant research. The two lowland gorillas in the New York Zoological Park are included in a report of the external genitalia published by Goss (3).

II. Subjects.

The gorillas studied at the Bronx Zoo are Oka, female, and Makoko, male. Since this study was made the Bronx Zoo has acquired a young female mountain gorilla, but no reference to it will be made in this report, except to list it in Table I. Little is known of the early history of Oka and Makoko. Both animals arrived in the Zoo on September 7, 1941, at which time they weighed 20 and 28

1 The success of this project was due in large part to the co-operation of the staff and keepers of the New York Zoological Park. Particular thanks are due Mr. Fairfield Osborn, Mr. John Tee-Van, Mr. Lee S. Crandall, Dr. L. J. Goss, Keepers Reilley and Quinn, and Mr. Sam Dunton, photographer.

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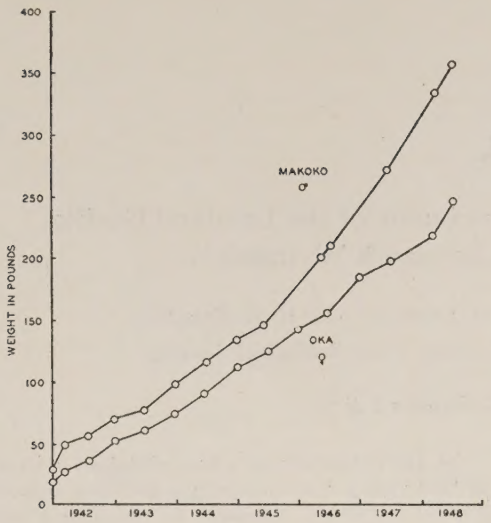
4 University of North Carolina, Chapel Hill, N. C.

5 City College of New York, N. Y. C.



TEXT-FIG. 1. Rate of growth of Oka and Makoko from time of arrival at the New York Zoological Park on September 7, 1941, until summer of 1948.

pounds respectively. Ages were estimated as one and three years on the basis of weight and bone structure. Text-figure 1 gives the data on the growth of the specimens from the time of arrival until the summer of 1948. The female was weighed, up to June, 1948, while on the keeper's back, the male's weight being merely estimated. In 1948 a Toledo balance was installed, on which the animals were weighed when they voluntarily mounted a platform.

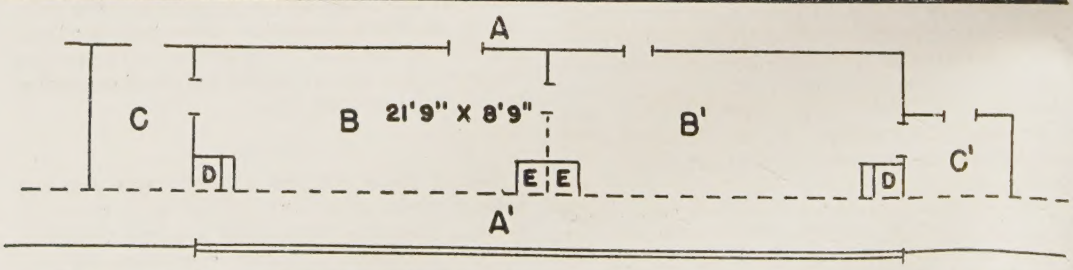
At the present time, Oka and Makoko are magnificent specimens. Makoko has a particularly brilliant coat and a notably prominent supra-orbital ridge. Oka is less impressively marked but is a splendid female example of the species. Both animals are active, healthy and strong. Indeed, Makoko's grip is so powerful that it has been necessary to replace the ¾-inch steel bars of the cage front, which he bent repeatedly. A steel horizontal ladder had to be removed from his cage when he tore it loose from its mooring. Oka is less destructive and retains her ladder.

III. Environmental Conditions.

The gorillas are housed in individual cages separated by a partition consisting of a solid metal access door and a double grill of steel bars. At the ends of each cage are doors leading to shift cages into which the animals are chased when the exhibition compartments are cleaned or repaired. The back wall of the living space is solid masonry with a recessed access door. Between the glass partition through which the public views the animals and the metal barred cage fronts is a passageway for the keepers. The internal features of the living compartments include a platform and a three-step staircase, with the platforms raised two inches from the floor, facing each other in front of the grill between the two cages. The staircases are at the ends near the shift cages. Oka's cage contains a metal horizontal ladder slung between the rear wall and the cage front at a height of three feet. Text-figure 2 shows the floor plan of the gorilla exhibition space.

IV. Daily Schedule of Animal Care.

Although the animals are on exhibition during the hours of 10:00 A.M. to 5:00 P.M. (except on Sundays when the visiting time is extended to 6:30 P.M.), the daily routine is more extensive. The overhead fluorescent lights are turned on at 8:00 A.M. when the keepers enter the building. Between 8:30 and 9:00 in the morning, the gorillas, each of whom has been in its own cage all night, are given their morning meal of skimmed milk and raw eggs. The ingredients are mixed and fed to each gorilla by tilting a can containing the mixture into the subject's mouth as the animal protrudes its lips through the bars of the cage front. Some half-hour to three-quarters of an hour later, the keepers move the gorillas to the shift cages. Separation and enclosure in the individual cages are effected by means of a stream of water. With the gorillas out of the way, the cages undergo thorough cleaning. Shortly before visiting time, the animals are released and are frequently permitted to remain together in one of the two cages for periods up to one hour. This opportunity for association occurs five



TEXT-FIG. 2. Floor plan of gorilla compartments in New York Zoological Park. **A, A'**, passageways for keepers. **B, B'**, exhibition cages for Oka (female) and Makoko (male), respectively. **C, C'**, shift cages. **D**, three-step stairs. **E**, platforms; right-hand platform used for weighing. **Thin line** indicates solid wall; **dotted line** indicates grill-front walls; **double line** indicates glass partition.

TABLE I.

Physical Characteristics of Gorillas in the United States.*

Name.	Location.	Form.	Sex.	Estimated age on September 1, 1949.	Known Weight.	Estimated Weight.
Oka	N. Y. Zool. Park	*gorilla*	F	9 yrs.	282 lbs.	
Makoko	N. Y. Zool. Park	*gorilla*	M	11 yrs.	408 lbs.	
Sumaili	N. Y. Zool. Park	*berengei*	F	20 mos.	20 lbs.	
Joanne	Central Park Zoo, N. Y. C.	*gorilla*	F	10 yrs.		190 lbs.
Carolyn	Central Park Zoo, N. Y. C.	*gorilla*	F	10 yrs.		190 lbs.
Bamboo	Philadelphia Z. G.	*gorilla*	M	23 yrs.		435 lbs.
Massa	Philadelphia Z. G.	*gorilla*	M	18 yrs.		400 lbs.
Bushman	Lincoln Park Zoo, Chicago	*gorilla*	M	21½ yrs.	542 lbs.	
Sinbad	Lincoln Park Zoo, Chicago	*gorilla*	M	20 mos.	38 lbs.	
Rajah	Lincoln Park Zoo, Chicago	*gorilla*	M	29 mos.		47 lbs.
Irvin Young	Lincoln Park Zoo, Chicago	*gorilla*	M	33 mos.	52 lbs.	
Lotus	Lincoln Park Zoo, Chicago	*gorilla*	F	43 mos.		75 lbs.
Miss Congo†	Chicago Z. P.	*gorilla*	F	16 yrs.		325 lbs.
Phil	St. Louis Z. P.	*gorilla*	M	10 yrs.		320 lbs.
Bobo	St. Louis Z. P.	*gorilla*	M	2 yrs.		44 lbs.
Big Boy	Cincinnati Zoo	*gorilla*	M	3 yrs.	35¼ lbs.	
Albert	San Diego Zoo	*gorilla*	M	6 mos.	9¾ lbs.	
Bouba	San Diego Zoo	*gorilla*	F	10 mos.	12½ lbs.	
Bata	San Diego Zoo	*gorilla*	F	8 mos.	10¾ lbs.	
Phil	Colorado Springs, Col.	*gorilla*	M	4 yrs.		40 lbs.
Gargantua	Ringling Bros. Circus	*gorilla*	M	17 yrs.	550 lbs‡	
Mtoto	Ringling Bros. Circus	*gorilla*	F	16 yrs.	438 lbs.‡	

* On October 31, 1949, three young specimens of *Gorilla g. gorilla* arrived in New York. They were a male and a female weighing 12-14 pounds, and a female weighing about 40 pounds. At the time this paper went to press they were still in the hands of Henry Trefflich, an animal dealer.
† Died Sept. 22, 1949.
‡ 1947 weight.

or six times a week and is the only occasion on which the animals are in unrestricted contact with each other. From the time of separation until the main feeding of the day at approximately 2:30 P.M., the gorillas are unattended except insofar as the keepers play with them while passing in front of the cages. The typical afternoon meal consists of carrots, celery, oranges, apples, grapes, bananas, beets, beans, sweet-potatoes, cabbage, onions, cherries and other seasonable fruits and vegetables. All food is fed raw and supplied through the front bars of the cages. Water, *ad lib.*, is available to each animal from a continuously running spigot which empties into a trough running along the back wall of each cage. At 5:30 P.M. the lights are turned out and the gorillas remain unattended until the next morning.

V. Observational Procedures.

Preliminary study of the gorillas was started at the beginning of May, 1948. One of the writers (B.F.R.) visited the Primate House at the Zoo on two days of each week and observed the gorillas for one hour. The times selected were in the early morning when the keepers placed the two gorillas in one cage, and in the late afternoon, at about 3:30 P.M. following the afternoon meal. At the later time, the animals were in separate cages.

As a result of the work during May and early June, a list was evolved on which both quantitative and qualitative indices of behavior could be noted. The inventory consisted of 42 items divided into five categories: posture and locomotion; eating, drinking and elimination; self-oriented activity (play?); inter-individual behavior; and observer-oriented behavior. The sheets of the check list were divided into 10 columns, each of which was used for a three-minute period of observation during the total 30 minute duration of the observational session. Thus it was possible to arrive at the total amount of each of the 42 types of behavior during the 30-minute period and also to determine the sequence of behavior during the period. Additional space was provided for running comments on the activity of the gorillas and for additional notes.

The observers worked in pairs and rotated the pairing so that a measure of control over reliability of observation was possible. There was joint discussion of the meaning of each term on the check-list so that the observers would agree on how to label the activity observed. The problem of the animal's reaction to the observer was considered and it was decided to standardize the position of the observers. Since the gorillas are a very popular exhibit and attract large crowds of spectators, the public exhibition space was used as the location for the observers who sat in pairs in front of the glass partition opposite

the communicating grill between the two cages.

Because the activity of the gorillas varied considerably with the time of day, the number of visitors, the daily routine and other variables, it was decided to distribute the 30-minute observation periods over the whole working day of the animal. However, since the gorillas were allowed to be in the same cage with one another only in the early morning, there was a greater concentration of sessions between 9:00 and 10:00 A.M. The total number of observations made during these hours was 10 one-half hour periods. Sixty-eight sessions were devoted to taking notes on behavior of the animals in isolation. During these 68 periods, it was possible to get data on both Oka and Makoko so that each animal was studied an equal number of times. Every hour between 10:00 A.M. and 6:00 P.M. was covered. In addition to these systematic observations which started in July and lasted through the middle of August, 1948, each experimenter observed the gorillas several hundred times while passing through the Primate House to and from other areas in the Park. Any deviant behavior or peculiar activities were noted and added to the record.

VI. Results and Discussion.

Two factors limit the analysis of the data. In the first place, quantitative analysis affords very little insight into the problem at hand. The purpose of this study was to obtain information which would serve as a starting point for further investigation of the gorillas at the Bronx Zoo, particularly as they become physiologically more mature and show active sex and social behavior. In the second place, it was thought desirable to point to both the similarities and differences between our gorillas and those at the San Diego Zoo described by Carpenter.

In this comparison, there are many difficulties and dangers arising from two sources. In the first place, the gorillas belong to different sub-groups, ours being lowland and Carpenter's mountain specimens. Other variables in this category include age and sex differences between the two sets of observed gorillas. In the second place, it is necessary to stress the differences in the environmental setting in which the San Diego and Bronx gorillas carried out their daily activity. At San Diego, the two male gorillas were housed in outside cages equipped with tree trunks for climbing and various devices which could be manipulated by the animals, for instance logs, swings, ropes, tires, etc. In addition, the experimenter could insert objects into the gorillas' surroundings and study the effect of such introductions. At the Bronx Zoo, the separation of the gorillas from the public was much more rigorous and the cages much more bare. In interpreting the comparative findings, the obvious individual and environmental differences must be kept in mind. However, despite these limitations, the comparison of the two groups should be of value, if only to emphasize the danger of generalizing from any set of observations.

With the restrictions specified above, the data in Table II represent the basic observations made upon the two gorillas at the Bronx Zoo. Where information comparable to that obtained by us was derivable from Carpenter's San Diego observations, it has been included in the Table. The discussion of the data in Table II will follow the general categories outlined above.

A. Posture and Locomotion.

Posture and general locomotion seem fairly well established as invariant gorilla patterns. Both Carpenter's mountain and our lowland gorillas exhibited the same type and frequency of gross motor activity. Walking, running, standing and sitting were characteristically alike for Oka, Makoko and the San Diego pair. Differences were noted in the frequency of observed sleep and in swinging by the hands. Both of these differences may be the resultant of variable environmental and observational procedures. It was not feasible for us to observe night behavior, and swinging was made difficult for Oka and Makoko by the absence of a place suitable for that kind of activity. The complete absence of nest-building in the Bronx pair is also related to the lack of adequate materials. Both Carpenter and Yerkes report that it was a fairly common behavioral pattern in their subjects.

The observations on handedness in the Bronx gorillas are not comparable to other studies since this item was not listed by Carpenter. Oka was observed to make differential use of her hands on 313 occasions and Makoko 184 times. In both animals, the right hand was more frequently employed regardless of the nature of the activity. The frequency of use of this hand was 54% as compared with the report by Yerkes (6) who found that Congo used her right hand some 66% of the time. In Congo's case the left foot was preferred to the hand, whereas in our gorillas there was relatively little pedal manipulation.

B. Eating, Drinking and Elimination.

In the presence of an abundance of food, Oka and Makoko both showed a form of behavior somewhat akin to the hoarding of rats and lower mammals. The gorillas would sweep the food into a heap with either the hands or feet. The heaped food was then examined, tossed around or eaten. This behavior is not mentioned in any other report on the gorilla and may well be the unique result of the absence of manipulatible material in the cages in the Bronx Zoo. Placing of the longer-stalked fruits and vegetables on the heads of the gorillas was a frequent aftermath of the in-gathering of the material.

An interesting aspect of the behavior of the isolated animals was a relatively infrequent passage of food from Oka to Makoko through the bars of the intercommunicating grill between the two cages. The initiation of this activity usually came from Oka and was noted particularly on the several occasions when Makoko had been deprived of his usual rations because of diarrhea or other health considerations. In such circumstances, Oka was observed forcing potatoes and cabbage through the double grill. Makoko did not seem to be particularly interested in the inserted foods. This behavior was seen on three occasions.

The drinking of water is a form of behavior common both to our animals and to those studied by Carpenter. According to Yerkes, Congo drank but little water. The manner of drinking in the Bronx animals was to bend over the fountain and suck the water into the mouth. Although there was no opportunity to study comparative satisfaction from milk and water, it is the opinion of the authors that the milk-egg liquid was preferred.

Regurgitation of the milk-egg mixture was almost invariable. Following the feeding the animals would typically squat on their haunches, lean forward, and regurgitate some if not all of the milk. The gorillas then would examine the liquid manually and eventually bend all the way and lick up the regurgitated material. The time interval after ingestion varied somewhat but was in the neighborhood of 45 seconds. Some chemical changes took place during the brief digestive stay for the milk was usually curdled. This pattern is seen not only in the gorillas at the Bronx Zoo but also in the chimpanzees. Whether or not this is a primate characteristic and analagous to the similar behavior of the pre-socialized human infant or whether it is unique to the subjects in captivity remains a matter for further research.

Voided fecal material was commonly handled both by Oka and Makoko and frequently was used to throw at the keepers, the observers or the public. Handling was casual and seemingly tactually motivated, for the feces were not examined nor used except for throwing. Since the keepers made heroic efforts to keep the cages clean, the opportunities for greater concentration on feces were limited. Carpenter makes no mention of this type of behavior. Urination was a casual affair and no localization of territory for this or for defecation was noted.

C. Self-oriented Activity.

Self-manipulation of parts of the body was a common form of activity in both Oka and Makoko. The parts of the body selected for handling or fingering were not consistent, with the exception of the lack of attention to or focus on the external genitalia. The major phase of activity during which handling was observed was while the gorillas were lying on their backs or stomachs, when parts of the body such as the lips, ears, eyebrows and nose would be held. The absence of genital manipulation may well be the result of the small size of the external genitalia of the gorilla, as described by Carpenter and Goss.

Manipulation of objects in the environment is a frequent finding wherever gorillas have been studied. Carpenter and Yerkes mention this behavior pattern and it was noticeable in the animals at the Bronx Zoo. The female, Oka, showed some tendency to manipulate and examine with greater frequency than her cage mate. In the absence of a variety of objects to examine, the frequency of occurrence of this activity is all the more remarkable.

The attitude of the gorillas toward the water fountain has already been described. An observable difference was noted in the behavior toward drinking water and that emanating from the pressure hoses used in cage cleaning. As indicated above, in the discussion of daily routine, water was used to separate the gorillas and to urge them toward the shift cages. The initial reaction to the stream from the hoses was retreat and excitement. However, once wet, the animals would face into the water and jump up and down. The keepers reported that the animals would on occasion approach more closely to the nozzle of the hose when thoroughly wet. No shaking of the body after the bath was seen during the periods of observation.

Self-grooming does not seem to be a dominant activity in the lives of either the San Diego or New York gorillas. To what extent the absence of this form of self-manipulation is a function of the cleanliness of the environment and the animal is not established by our observations but, as will be noted later, grooming as a pattern of behavior is markedly less present in the gorillas under study than in other primates at the Zoo.

D. Inter-individual Behavior.

The data in this section were obtained during those periods when the animals were together in the same cage. To the extent that the opportunity for such interaction was limited, the enhancement of activity during the periods of joint occupancy of the cage may be a function of the limitation of time during which the two animals could interact.

Both in Carpenter's study and in ours, the major forms of inter-individual activity were running, chasing and wrestling. These behavior patterns were well marked and almost stereotypical in appearance. Chasing was especially vigorous when the cage floor was wet and the gorillas spent much time sliding in a pronograde posture from one end of the cage to the other. Initiation of this activity was fairly evenly divided between Oka and Makoko. Wrestling, too, was not started consistently by either male or female. A dominance pattern was not apparent.

The sequence of individual motor acts in

TABLE II.

Comparative Behavior of Oka, Makoko and San Diego Gorillas.*

Behavioral Classification	Frequency of Occurrence in San Diego	Oka	Makoko
A. *Posture and Locomotion*			
Walking, pronograde	+ + +	+ + +	+ + +
Walking, upright	+	+	+ +
Running, pronograde	+ + +	+ + +	+ + +
Running, upright	ND	+	+
Standing, pronograde	+ + +	+ + +	+ + +
Standing, upright	+	+	+
Sitting	+ + +	+ + +	+ + +
Climbing	+ +	+	+
Swinging by hands	+ +	+	+
Hanging	+	+	+
Sliding	+ + +	+ +	+ +
Left-handedness	ND	46%	46%
Right-handedness	ND	54%	54%
Lying down	+ + +	+ + +	+ + +
Sleeping	+ +	+	+
Nest Building	+	NP	NP
B. *Eating, Drinking and Elimination*			
Gathering food in heaps	ND	+ +	+
Sharing food with cage mate	O	+	+
Drinking water	+ + +	+ +	+ + +
Drinking milk	+ + +	+ +	+ +
Regurgitation of milk	ND	+ +	+ +
Handling of feces	ND	+	+
Attention to urination	ND	+	+
C. *Self-oriented activity (Play?)*			
Self-manipulation (non-genital)	+ +	+ +	+ +
Manipulation of genitalia	O	O	O
Manipulation of objects	+ + +	+ +	+
Manipulation of food (non-eating)	ND	+ +	+ +
Attitude toward stream of water	positive + +	+	+
Self-grooming	+ +	+	+
D. *Inter-individual behavior*			
Chasing	+ + +	+ + +	+ + +
Wrestling	+ + +	+ + +	+ + +
Grooming	+ +	+	+
Inspection and manipulation of genitalia	O	O	+
Presenting	O	O	O
Mounting	O	O	O
Pelvic thrusts	O	O	+
Chest thumping	+ +	+	+ +
Vocalizing	+ +	ND	ND
Dominance	+	+	+
E. *Observer-oriented behavior*			
Throwing of feces	ND	+	+ +
Throwing of non-fecal material	ND	+	+
Attentional responses	positive + +	negative + +	negative + +
Vocalization	+ +	ND	ND

* Key to symbols:

O—Never observed or reported
+—Little in frequency or amount
+ +—Some or fairly frequent
+ + +—Great deal, very frequent
ND—No data reported
NP—Not possible in the environment

the wrestling behavior was free of patterning and seemed to consist of random grappling at the anatomical point nearest to the initiator of the behavior. When the actions of either animal seemed to approach the point at which roughness would ensue, the animal at the moment on the receiving end would detach itself and a period of resting would follow. Of all the behavior noted in this study, wrestling was the most dramatic and illustrative of the great strength of the gorillas. As a rule, there were few vocalizations during the bouts.

Social grooming, certainly, does not seem to be as predominant in the behavior of the gorillas as in the case of other representatives of the great apes or other primates. Carpenter likewise observed little of this sup-

posedly socially oriented activity. It is possible that in the four animals for which data are available, the age and sex differences were not sufficiently well established to facilitate the appearance of this type of social interaction. It may also be possible that there is a real species difference in such behavior.

Genital manipulation and exploration in the paired situation was not frequently observed. It was seen only three times in Oka and Makoko and was not reported for the San Diego pair. In the Bronx specimens, the initiator was always the male. This may be a reflection of the relatively greater maturity of Makoko. So, too, in our gorillas, mounting and pelvic thrusts as precursors of mating behavior were almost completely absent during the periods of observation in New York. Carpenter saw none of this at San Diego, but his animals were both males. The one instance of pelvic thrusts by Makoko occurred during a wrestling bout and was not repeated nor invited by Oka.

Chest-thumping was much more prevalent during the periods of paired activity than when the animals were in their own cages. The causal sequences leading up to the thumping could not be determined for Oka and Makoko although the observers were all of the opinion that the behavior was socially oriented and significant. Some writers have suggested that thumping of the chest is a sign of well-being and general euphoria. Yerkes states that the behavior is a sign of "impatience or other mild dissatisfaction." There was clear evidence of neither causal sequence in our observations. The range of situations during which the thumping was observed varied so widely that no specific factor can be assigned as the reason for its existence. The only statement that can be made from our data is that the male, Makoko, engaged in chest-thumping more frequently than did Oka and accompanied the beating with vocalizations more frequently than his companion.

In the absence of sound-recording devices, description of vocalization is difficult. Furthermore, the public space was somewhat soundshielded by the glass partition separating the animals from the observers. In our experience the occurrence of this activity was less than that mentioned by Carpenter.

E. Observer-oriented Behavior.

The types of audience-attentive behavior observed in the Bronx Zoo consisted mainly of the throwing of feces or food at the glass plate between the cage and the visitors. The same aggressive behavior was noted during an attempt to get photographs of the animals. Visitors invariably tried to attract attention from the gorillas by tapping on the glass partition and by yelling. The effect of such devices was negligible. This difference between our data and Carpenter's may well be the result of the more restrictive conditions of the gorillas' environment in the New York Zoo.

VII. Summary.

This report describes the behavior of two pre-adolescent lowland gorillas in the New York Zoological Park during the summer of 1948. Oka, then an eight-year-old female, and Makoko, a ten-year-old male, were observed in their regular living cages when alone and when placed together.

A check-list was prepared and regular half-hour periods of observation were systematically made. Significant behavioral items were compared for the sessions when the animals were alone and when they were together. Comparisons were also made with the data collected by Carpenter from two male mountain gorillas in the San Diego Zoo.

The descriptive material obtained during the period of observation should serve as a base line from which to note variations arising from the maturation of the two gorillas in the years to come.

References.

1. Bingham, H. C. 1932. Gorillas in a native habitat. *Carnegie Inst. Wash. Publ.*, No. 426. Pp. 66.

2. Carpenter, C. R. 1937. An observational study of two captive mountain gorillas (Gorilla beringei). *Human Biol.*, 9, 175-196.

3. Goss, Leonard J. 1947. The external genitalia of the gorilla, *Gorilla gorilla gorilla* (Savage & Wyman). *Zoologica*, 32, 97-99.

4. Leister, Claude W. Gorillas. New York Zoological Society, Popular Series No. 4.

5. Valker, A. 1931. La vie du gorille au Gabon. *Bull. Mus. Nat. d'Histoire Nat.*, 3.

6. Yerkes, R. M. The mind of a gorilla. (a) *Genet. Psychol. Monogr.* 1927, 2, 1-193. (b) *Genet. Psychol. Monogr.*, 1927, 2, 375-551. (c) *Comp. Psychol. Monogr.*, 1928, 5, 1-92.

EXPLANATION OF THE PLATES.

PLATE I.

FIG. 1. Makoko, the male lowland gorilla in the New York Zoological Park. Estimated age, 11 years; weight, 408 pounds.

PLATE II.

FIG. 2. Oka, the female lowland gorilla in the New York Zoological Park, is still friendly and gentle with her keeper at the estimated age of 9 years. Her weight is 282 pounds.

FIG. 3. Oka playing with her keeper.

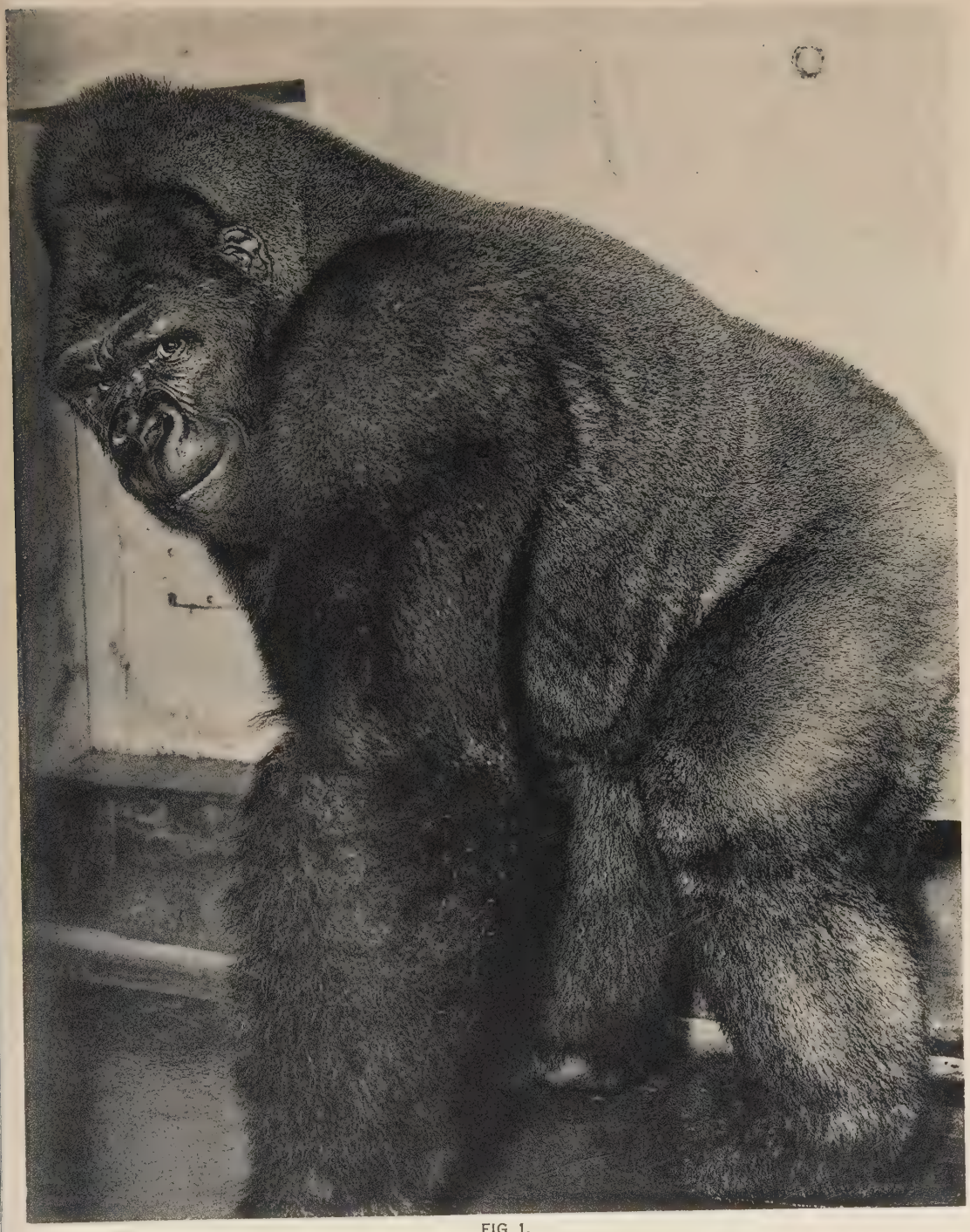


FIG. 1.

THE BEHAVIOR OF TWO CAPTIVE SPECIMENS OF THE LOWLAND GORILLA, GORILLA GORILLA GORILLA (SAVAGE & WYMAN).

FIG. 2.

FIG. 3.

THE BEHAVIOR OF TWO CAPTIVE SPECIMENS OF THE LOWLAND GORILLA, GORILLA GORILLA GORILLA (SAVAGE & WYMAN).

14.

Migration of Papilionidae at Rancho Grande, North-central Venezuela.[1]

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(Plate I; Text-figure 1).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows; Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the water-shed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

For an account of Portachuelo Pass, together with a general introduction to the groups of migrating insects and migrating factors see "Insect Migration at Rancho Grande," by William Beebe, *Zoologica*, 1949, Vol. 34, No. 12, pp. 107-110.

In Volume 26 of *Novitates Zoologicae*, W. J. Kaye has a paper entitled "A Geographical Table to show the Distribution of the American Papilios." Under the heading "Venezuela, North," (pp. 352-355), the author lists thirty-one species. In a letter Dr. Rene Lichy of Caracas sends me a list of thirty-one species of this family which he has collected in northern Venezuela. A continuation of this coincidence is that each list contains seven species not found in the other list.

Both lists contain all the species which we took migrating through Portachuelo Pass, with the single exception of *crassus* which Lichy does not mention.

In the limited width of twenty meters of Portachuelo Pass, and allowing a height of net reach of a maximum of five meters, we captured seventeen species of *Papilio*. This area may be considered, not unrealistically nor unconservatively, as, at the most, a millionth of the extent of north Venezuela. Yet within this relatively microscopic bit of Andean air, we secured almost half the papilios so far recorded from the entire northern part of the country. Thus, in the consideration of this family of butterflies, we are made to realize the wide-spread, impelling, migrational force affecting this group of insect life.

So much of this migration—its causes and extent—is at present unknown, that every verifiable fact is of value. Reviewing the known distribution of the seventeen species of *Papilio* migrants, we find that most of them extend from Mexico to Paraguay, south Brazil or Argentina. The distribution of the subspecies, however, presents a very different picture, and a very significant one in its over-all pattern. In twelve out of the seventeen, the subspecific range is confined to Colombia and Venezuela, with a few extensions to adjacent territory. Thus we may expect to find the northern point of origin of the movement of these forms a relatively short distance away.

The twelve subspecies of *Papilio* with limited distribution are as follows:

anchises osyris
anchisiades anchisiades
agesilaus agesilaus
arcas arcas
cleotas coroebus
erithalion zeuxis
lycophron hippomedon
paeon thrason
polyxenes americus
protesilaus archesilaus
sesostris tarquinius
torquatus orchamus

1 Contribution No. 852, Department of Tropical Research, New York Zoological Society.

The remaining five forms of *Papilio* with wider distribution are:

belus varus
crassus
phaon
polydamus polydamus
thoas neacles

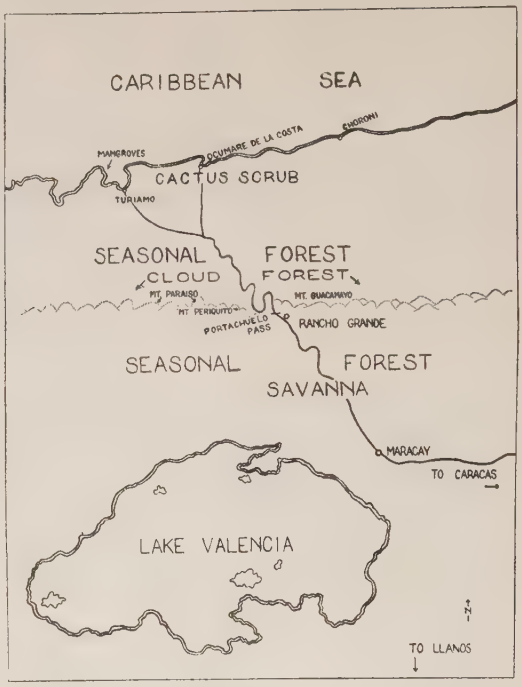
Let us take as an example *Papilio agesilaus agesilaus* or, as I called it before identification, Small Zebra Swallowtail. I recorded seven individuals captured and fifty-eight seen with certainty. Added to this number were the many papilios glimpsed too briefly, flying too high or too fast to be recognized as to species, and also those which must have passed during the hours of our absence from the pass. It was heartbreaking to realize what a minute fraction we could honestly record by sight identification, yet there is no other way, at present known, to glean definite, general knowledge of this phase of the lives of these splendid insects. Without exception, all sight-named species were subsequently confirmed or discarded by comparison with captured, definitely classified specimens.

In this as in some other species, the small number of records from the year 1946 and their entire absence from 1945 by no means indicates the absence of the species on migration, but only reflects our non-recognition of the importance of the Portachuelo Pass migration during the early years, and consequent slight attention paid to this phenomenon. An ultimate summary of the relatively few, disconnected observations made during 1945 and 1946 reveals a general movement on a scale equal in magnitude and as all-embracing of insect orders as we recorded during 1948.

The mere recording of the capture of seventeen species of *Papilio* on migration is a worth-while fact, and when more and more individuals are taken on suceeding days and weeks the phenomenon is enhanced in interest. In few or in large numbers the insects continue to fly past, slowly or circling or alighting out of reach. As in the case of many other organisms, the time has come when sight records must be used to supplement specimens in net, envelope and cabinet. Ornithologists in general and British entomologists in particular have gone far in sight identifications, while at the same time maintaining as perfect accuracy as possible with man's fallible eyesight and only too human brain.

At the end of our many months of collecting and observation at the pass, I found, in my Journal, a significant assemblage of shorthand names of papilios. They were, of course, essentially personal, stimulated by mental comparisons with swallowtails familiar to me elsewhere, or in the case of strange tropical forms, by outstanding wing shapes, size, patterns and colors.

Lepidopterists recognize three "natural groups" into which papilios may be divided.



TEXT-FIG. 1. Map showing location of Rancho Grande, Portachuelo Pass and surrounding territory.

These are based on various factors such as larvae, pupae, microscopical imaginal distinctions and/or food-plants. Our migrant species fit into these three groups as follows: ARISTOLOCHIA: *sesostris, erithalion, anchises, arcas, polydamus, belus* and *crassus*. FLUTED: *polyxenes, thoas, paeon, lycophron, anchisiades, torquatus* and *cleotas*. KITE: *phaon, agesilaus* and *protesilaus*.

Consideration of this arrangement shows no logical, technical or scientific agreement. This is only to be expected in sight identification, which can take no account of sexual relationships, or parallelisms, or the superficial resemblance brought about by mimicry.

After final identification of the seventeen species of *Papilio* migrants, I arranged mounted specimens of all in a large insect drawer, placed this upright on a chair in good light and studied them from a distance of ten meters. From this distance I made the following key:

A—WHITE AND BLACK
- a—Small: *agesilaus agesilaus*
- b—Large: *protesilaus archesilaus*

B—YELLOW AND BLACK
- a—Yellow-banded
  - Broad-band-plus-spot, small: *torquatus, orchamus*, male
  - Broad-band, medium: *lycophron hippomedon*, male
  - Narrow-band: *paeon thrason thoas neacles*

b—Yellow-spotted
Small: *polyxenes americus*
Medium: *polydamus polydamus*
Large: *cleotas coroebus*

C—Red and Black (Hindwing)
a—Cream-spot-forewing
sesostris tarquinius, female
erithalion zeuxis, female
anchises osyris, female
arcas arcas, female
torquatus orchamus, female
b—Green-spot-forewing
erithalion zeuxis, male
anchises osyris, male
arcas arcas, male
c—Black-forewing
anchisiades anchisiades

D—Green and Black
a—Green-forewing
sesostris tarquinius, male
b—Green-hindwing
phaon

E—Black (Dominantly)
belus varus
crassus
lycophron hippomedon, female

I compared this key with the names made up on the spot in the field, and found a gratifying agreement in species recognition. The differences were chiefly substitution for patterns and colors of the names of northern species suggesting resemblances, species with which I had long been familiar in the eastern United States. For example, *agesilaus agesilaus* was "small ajax or zebra," *polyxenes americus* was "small asterias," and *thoas neacles* was "cresphontes-like," etc.

I cite all this as in no way directly possible or in the same detail applicable for use by another observer, but merely to show a framework upon which can successfully be erected an observer's sight key. Further comments, in greater or less detail, will be found under the treatment of many of the species.

My special thanks go to Mr. Henry Fleming, entomologist of our Department of Tropical Research, for many direct observations and for frequent corroboration of my own. In addition I am beholden to him for looking up distribution data and for painstaking identification of all the species.

Papilio anchises osyris Felder.

Species Range: Colombia to Brazil, Bolivia and Paraguay.

Subspecies Range: Venezuela.

Field Characters: Both male and female indistinguishable in the field from *erithalion zeuxis*. Therefore all specimens observed and not taken are combined under the two species. Compared with *arcas arcas* the male lacks bright green forewing spot, and the female has a decidedly larger, 4-celled forewing cream spot.

Number and Sex: Both sexes taken; eight males, five females.

Date: April 13 to July 29.

Condition: All taken were fresh.

Record of Captures: 1945—July 15 (male), 18 (female). 1946—April 13 (male, km. 20). 1948—April 29 (male); May 1 (female), 31 (female); June 6 (male and female); July 17 (male, km. 30), 23 (male, km. 15), 29 (female at Pass, 2 males, km. 35).

Combined Sight Records: *anchises* and *erithalion*: (Total 62). 1946—May 27 (4 females); June 29 (2 females). 1948—May 26 (4 females); June 4 (11 females passed in 10 minutes), 15 (4 females resting on shrubs), 22 (5 seen); July 2 (12 females), 9 (14 males, 3 females), 29 (3 females).

Papilio anchisiades anchisiades Esper.

Field Name: Red-spot Black.

Species Range: Mexico to southern Brazil.

Subspecies Range: Colombia to Bolivia and Para (Brazil).

Field Characters: Black with red on hindwing. Closest in field appearance to wholly black *lycophron hippomedon*.

Number: 2 specimens taken, a male and a female.

Notes: This black-forewing-red-hindwing papilio came through the Pass with what were taken and identified as female *arcas arcas* and *anchises osyris*, all captured together.

Record of Captures: A male in frightfully worn condition collected on April 13, 1945, No. 45456. A second individual, a female, taken at the Pass May 1, 1948, No. 48474.

Papilio agesilaus agesilaus Guerin.

Field Name: Small Black-and-white Zebra Swallowtail.

Species Range: Mexico to Paraguay.

Subspecies Range: Magdalena Valley, Colombia, to northern Venezuela.

Field Characters: Unmistakable resemblance to our northern ajax or zebra. The only optically related species is *protesilaus archesilaus*, but the present species is much smaller (forewing 43 mm. as compared with 53 mm.). The difference easily recognizable when either species is close at hand or near other butterflies.

Number: Total recorded 58. Seven taken (48543, 48731, 481344, 481494).

Sex: Both sexes taken.

Date: From April 29 to July 26.

Frequency: Recorded on seventeen days. Moderately but markedly gregarious. Two-thirds of *agesilaus* were recorded in groups of 4 to 8, while one-third appeared singly or in twos.

Flight: Except when alarmed or fighting against a strong head wind, the flight was unhurried and wavering, always steadily south.

Condition: With one exception all that I saw hovering or resting at the Pass were in

good condition, with both long slender tails visible to the naked eye or through three-power binoculars. No. 481344, taken July 26, 1948, at kilometer 16, was badly mutilated, with one tail missing. Dissection revealed that this male had already mated.

Record: 1946—May 26 (2 seen), 27 (2 at Pass, 3 at km. 20), 30 (6 singly). 1948—April 29 (2); May 14 (1 taken), 21 (4 seen, 1 taken), 23 (1 taken), 24 (4), 26 (4), 31 (8); June 6 (1), 17 (2 taken), 19 (2); July 13 (4), 16 (2), 23 (1 taken km. 16), 24 (6), 26 (1 at Pass, 1 at km. 16).

Papilio arcas arcas Cramer.

Field Name: Green-spot (male). Two-celled-cream-spot (female).

Species Range: Mexico to Colombia, Venezuela and the Guianas.

Subspecies Range: Venezuela and the Guianas.

Field Characters: Closest to *anchises* and *erithalion,* from which it differs in the bright green forewing spot in the male, and the smaller, two-cell forewing spot in the female. It is also close to the exceedingly rare *torquatus orchamus.* From the male *sesostris tarquinius* this species differs in the red on the hindwing.

Number: Total recorded 277. Twenty-one taken.

Sex: Both sexes taken. In 1946 only females were seen or taken. In 1948 females were dominant from May 1 to June 17, and males from July 6 to July 22.

Date: May 1 to July 22.

Frequency: Recorded on 20 days: 1 (15 times), 2 (4 times), 4 (once), 6 (twice), 7, 13, 14, 16, 18, 29 and 85. Decidedly gregarious, occurring singly and in twos nineteen times, comprising one-fourteenth of the total number passing in larger numbers—from 4 to 85. As mentioned above, the sexes showed a decided segregation. The flocks were usually compact waves.

Flight: Rather low and fluttering.

Condition: Most of *arcas* observed were in fresh condition, decidedly unworn.

Extent of Migration: On four separate days specimens of this species were taken both at the Pass and at kilometer 20, well to the south, and at kilometer 35, half way to the coast to the north.

Record: 1945—July 3 (3 taken), 16 (2 seen, 1 taken, Limon). 1946—May 28 (27 seen, 2 taken), 29 (7 at Pass, 6 at km. 20), June 4 (female), 22 (female); September 7 (84 in half an hour, 1 taken). 1948—May 1 (female), 4 (6 females), 5 (male), 28 (female) 29 (female); June 6 (2 males, flock of 18 females), 17 (16 females flying low), 22 (male and female), 28 (28 females); July 6 (2 males), 9 (male caught and eaten by bat falcon, 21 males seen), 14 (7 males), 15 (11 males, 3 taken), 16 (13 seen, four fighting in midair), 19 (4 males, 1 taken km. 15), 22 (2 males, 1 taken km. 35).

Papilio belus varus Kollar.

Species Range: Mexico to Bolivia and Para (Brazil).

Subspecies Range: Guatemala to northern Venezuela and Ecuador.

Dichromatic Female, form *latinus* Felder.

Field Name: Greenish-hindwing-band Black.

Field Characters: Black, with a curved band of large, yellow-green spots on hind wing.

Number: Total recorded 19. Eight taken.

Sex: Females only taken.

Date: May 29 to August 4.

Frequency: Taken singly. Five once seen together.

Condition: Fresh.

Record: 1946—July 7 (1 seen km. 20). 1948—May 29 (1 seen); July 4 (4 seen at 8:30 A.M.), 14 (1 taken), 16 (3 taken), 21 (2 taken, 3 seen), 26 (1 taken, 2 seen km. 16); August 4 (1 taken).

Dichromatic Female, form *varus* Kollar.

Field Name: Cream-spot-forewing Black.

Field Characters: Irregular splash of yellow in forewing; hindwing blue-black.

Number: Total recorded 18. Three taken.

Sex: Females only taken.

Date: May 30 to July 26.

Frequency: On two occasions, five were seen together.

Condition: Fresh.

Record: 1948—April 29 (1 taken); May 30 (5 seen); July 8 (3 seen), 9 (2 seen alighted, 2 taken, 5 seen km. 31).

Papilio cleotas coroebus Felder, form *dione* Rothschild and Jordan.

Field Name: Large Asterias Swallowtail.

Species Range: Costa Rica to Brazil.

Subspecies Range: North Colombia and Venezuela.

Field Characters: Rather like a very large Asterias, or *polyxenes americus,* with forewing 67 mm. as compared with 40 mm. A very distinct species.

Number: Total recorded 19. One taken.

Sex: The single specimen taken was a female.

Date: May 26 to July 17.

Record: 1948—May 10 (4 seen), 26 (2 seen); June 6 (female taken, 2 others flying in company with three of the small *polyxenes americus*); July 10 (2 at Pass, 2 at km.15), 17 (3 at Pass, 3 at km. 30).

Papilio crassus Cramer, male form *lepidus* Felder.

Field Name: Black Philenor.

Species Range: Costa Rica south to Brazil.

Field Characters: Wholly black except for concealed bluish-white anterior border of hindwing.

Number: Total seen 23. One taken.

Record: A single male specimen of the form *lepidus* taken on July 21, 1948, No. 481538. Twenty more, distinctly seen, passed

at the same time, all out of reach. On the following day, July 22, two more of these black papilios were seen. No other record.

Papilio erithalion zeuxis Lucas.

Species Range: Costa Rica to Colombia and northern Venezuela.

Subspecies Range: North Venezuela and Colombia.

Field Characters: Both sexes indistinguishable from *anchises osyris*. Differs from *arcas arcas* in male lacking forewing green spot, and female with larger, 4-celled forewing cream spot.

Number: Total number taken 14.

Sex: Both sexes taken.

Date: June 29 to July 24.

Condition: All freshly emerged.

Record of Captures: 1945—July 3 (female taken, Limon). 1946—June 29 (female, km. 20); July 7, 8 and 10 (Each day 1 female taken, km. 20). 1948—July 9 (3 males, km. 31), 14 (male), 15 (male), 17 (2 females), 23 (female, km. 15), 24 (female).

For joint sight identification records with *anchises osyris*, see under latter species.

Papilio lycophron hippomedon Felder.

Field Name: Male, Broad-band Medium Turnus. Female, Black Troilus-like Swallowtail.

Species Range: Mexico south to Argentina and Uruguay.

Subspecies Range: Colombia and northern Venezuela.

Field Characters: Male can be confused only with the very rare, smaller, yellow-spot *torquatus orchamus;* female recalling a melanistic *troilus* or *phaon* with black hindwings.

Number: Total recorded 20. Eight taken.

Sex: Both sexes taken.

Date: May 10 to July 20.

Record: 1946—May 27 (2 at Pass, 2 km. 20, all males). 1948—May 10 (3 males seen), 21 (female taken), 23 (male taken), 24 (male taken), June 6 (2 females taken), 17 (2 males taken), 29 (4 males seen); July 10 (male seen), 20 (male taken).

Papilio paeon thrason Felder.

Field Name: Rare Cresphontes-like Swallowtail.

Species Range: Mexico south to Argentina and Uruguay.

Subspecies Range: North Colombia and Venezuela.

Field Characters: Indistinguishable in the field from *thoas neacles*, but as only a single specimen of *paeon thrason* was taken, compared with more than one hundred of *thoas*, I am assuming that all Cresphontes-like papilios observed were of the more abundant species.

Record of Capture: A single male taken on May 23, 1948, No. 481539, in extremely torn and worn condition. It was captured at the Pass at 12:30 P.M., the day being warm and sunny with a Force 4 wind from the south.

Papilio phaon Boisduval, aberration *metaphaon* Butler.

Field Name: Philenor-like Swallowtail.

Species Range: Mexico to Ecuador and Venezuela.

Field Characters: This is the only black papilio with green on the hind wings.

Number: Total recorded 254. Seven taken.

Sex: Both sexes taken.

Date: April 13 to July 21.

Record: 1945—May 24 (1 taken). 1946—(September 9, numbers of these black papilios with large green spot on the hind wings were flying too high to catch. Several alighted and allowed detailed study with Number three glasses. Counted 228 and missed many more.) 1948—April 13 (male taken km. 20), 16 (male taken), 27 (male taken, km. 20), 29 (female taken at Pass); July 21 (2 taken, 19 seen).

Papilio polydamus polydamus Linnaeus.

Field Name: Medium Asterias Swallowtail.

Species Range: South Atlantic states, West Indies and south to Argentina.

Subspecies Range: Georgia south to Buenos Aires.

Field Characters: Differs to the eye from *polyxenes americus* in the field by the single instead of double line of yellow spots across all wings. Another distinction is the larger size.

Number: Total recorded 177. Nine taken.

Sex: Both sexes taken.

Date: May 15 to July 26.

Frequency: Decidedly gregarious. One-eighth passed singly or in a scattering up to five individuals. Seven-eighths were observed in flocks of ten to forty-eight.

Record: 1946—May 27 (2 seen). 1948—May 15 (5 seen), 29 (female taken); June 6 (female taken), 22 (11), 30 (female taken, 48 passing, 2 seen at km. 21). July 9 (female taken), 10 (2 males taken, 16 seen. 2 taken km. 31), 11 (14 flurry, 1 single), 14 (1 taken, 23 seen), 17 (10 seen km. 30), 18 (3), 19 (3), 22 (3 km. 35), 26 (27 seen).

Papilio polyxenes americus Kollar, form *melasina* Rothschild and Jordan.

Field Name: Small Asterias Swallowtail.

Species Range: Canada south to Cuba and Peru.

Subspecies Range: Colombia, Venezuela and northern Peru.

Field Characters: Under a new name this proved to be the same species as our northern Asterias. The only other resembling migrant butterfly was the markedly larger *polydamus polydamus*.

Number: Total observed 34. Although observed on ten occasions during two seasons, only three specimens were taken.

Date: March 25 to July 20.

Frequency: 1, 1, 1, 2, 2, 2, 3, 3, 3, 6, 6.

Note: Three perfect specimens on June 5, after rain, clung to the extreme ends of large leaves. The wings were flat and expanded, with the fore edge straight across so that the transverse band and spots were continuous.

Record: 1946—March 25 (1 taken, km. 21); April 19 (1 taken, km. 21); May 28 (2 seen at Pass). 1948—April 29 (3 seen); May 4 (6 flying together), 28 (2 seen); June 5 (3 seen), 6 (3 seen); July 19 (6 seen), 20 (1 taken at Pass), 22 (6 seen at km. 35).

Papilio protesilaus archesilaus Felder.

Field Name: Large Zebra Swallowtail.

Species Range: Mexico to Paraguay.

Subspecies Range: Colombia, northern Venezuela and western Ecuador.

Field Characters: Larger than (forewing 53 mm. as compared with 43 mm.) but in general similar to *agesilaus*. Size difference quite apparent when near, but not when flying high, away from other known butterflies. At least fifteen individuals were not counted because of uncertain sight identification.

Number: Total recorded 42. Three taken (48543).

Sex: Males only were taken. The female seems to be quite unknown.

Date: Recorded on migration from April 29 to July 19.

Frequency: The relative gregariousness corresponds to that in *agesilaus*. More than five-sixths were in 4 to 12 groups, and six only seen as solitary or dual migrants.

Condition: All observed in detail appeared fresh and perfect.

Additional Notes: The flurry of 12 large zebras on May 30, were in a compact body, and at a time when neblina and rain, while light, were continuous enough to discourage all other migrants. Yet these great swallowtails flew steadily at a height of about 12 feet, up to and through the Pass and down into the fog on the south slope.

The actions of six which passed on May 26 were typical. All flew slowly and with slightly wavering flight at 10 feet, until I swooped futilely at them with the net when all swerved sharply out and down, two penetrating the underbrush and working their way separately through the Pass before rising into the free air again. Three were followed with the glasses far down the south slope.

Record: 1946—May 27 (1 seen, 1 at km. 20), 29 (4 seen, 1 taken). 1948—April 29 (4); May 1 (3), 4 (1 taken), 10 (1), 21 (5 seen, 1 taken), 26 (6), 30 (12); July 19 (1 at Pass, 1 at km. 15).

Papilio sesostris tarquinius Boisduval.

Field Name: Male, Green-spot Black.

Species Range: Mexico to Bolivia and central Brazil.

Subspecies Range: Panama, Ecuador, northern Venezuela.

Field Characters: Male to be confused only with male *arcas arcas*, but wholly lacks the hindwing red.

Number: Total recorded 39. Three taken.

Sex: Males only taken.

Date: April 30 to July 20.

Frequency: 1, 4, 5, 6, 23.

Condition: All freshly emerged.

Record: 1948—April 30 (1 taken); June 10 (4 seen), 17 (6 seen), 22 (22 seen, 1 taken); July 20 (4 seen, 1 taken).

Papilio thoas neacles Rothschild and Jordan.

Field Name: Common Cresphontes-like Swallowtail.

Species Range: Texas to Buenos Aires.

Subspecies Range: Nicaragua to Ecuador, Venezuela, Trinidad and the lower Orinoco.

Field Characters: Cresphontes-like. Unidentifiable, even at close range, from *paeon thrason*, but only a single specimen of the latter was taken in two years of collecting.

Number: Total recorded 105. Nine taken.

Sex: Both sexes taken.

Date: May 4 to September 8.

Frequency: Usually seen passing in small groups, five to eight, maximum sixteen. Strong flyers, difficult to capture, but occasionally alighting, affording opportunity for a good look.

Record: 1946—May 4 (male taken, km. 20), 27 (16 seen); July 7 (female taken, km. 20); September 8 (3 seen). 1948—April 29 (3 seen), 30 (3, km. 26, headed for Pass); May 1 (4), 10 (2), 11 (2), 15 (4 seen, 1 taken), 23 (8 seen, male taken), 26 (6), 31 (1 seen); June 6 (3 taken, male, 2 females. Eggs protruding from females), 10 (5), 18 (8), 22 (6), 29 (4), 30 (5); July 2 (5 seen), 9 (2 at Pass, 6 km. 31), 13 (male taken), 19 (3 seen, 1 taken km. 18).

Papilio torquatus orchamus Boisduval.

Field Name: Male, Small Yellow-Band-and-Spot. Female, mimic of *arcas*.

Species Range: Mexico to Bolivia, Brazil and Paraguay.

Subspecies Range: Colombia and northern Venezuela.

Field Characters: Male somewhat similar to but smaller than male *lycophron hippomedon;* female very close to female of *arcas arcas*. The large, separate, anterior yellow spot on forewing of the male distinguishes it from the solid band of *lycophron*.

Number: Two males were seen, and two females taken.

Sex: Both sexes seen, female only taken.

Dates: May 1 to July 2.

Record: On May 1, 1948, I watched two new papilios fighting in the Pass. One flew down and alighted just out of reach, and the other soon followed. I made a detailed description of them, recording them as yellow-

banded-with-spot, tailless papilio. Not until our return north were we able to identify the insects by comparison with a male *torquatus* taken at Caripito.

On May 26 and again on July 2, 1948, a female was taken. These were badly rubbed and torn, whereas the males I saw were freshly emerged.

EXPLANATION OF THE PLATE.

Plate I.

Seventeen species of butterflies of the genus *Papilio* taken as migrants at Portachuelo Pass, Rancho Grande, north-central Venezuela.

Fig. 1. *sesostris tarquinius* (male).
Fig. 2. *sesostris tarquinius* (female)
Fig. 3. *erithalion zeuxis* (male).
Fig. 4. *erithalion zeuxis* (female).
Fig. 5. *anchises osyris* (male).
Fig. 6. *anchises osyris* (female).
Fig. 7. *arcas arcas* (male).
Fig. 8. *arcas arcas* (female).
Fig. 9. *polydamus polydamus.*
Fig. 10. *belus varus* form *latinus.*
Fig. 11. *belus varus* form *varus.*
Fig. 12. *crassus* form *lepidus.*
Fig. 13. *polyxenes americus* form *melasina* (male).
Fig. 14. *polyxenes americus* form *melasina* (female).
Fig. 15. *thoas neacles.*
Fig. 16. *paeon thrason.*
Fig. 17. *lycophron hippomedon* (male).
Fig. 18. *lycophron hippomedon* (female).
Fig. 19. *anchisiades anchisiades.*
Fig. 20. *torquatus orchamus* (male).
Fig. 21. *torquatus orchamus* (female).
Fig. 22. *cleotas coroebus* form *dione.*
Fig. 23. *phaon* aberration *metaphaon.*
Fig. 24. *agesilaus agesilaus.*
Fig. 25. *protesilaus archesilaus.*

MIGRATION OF PAPILIONIDAE AT RANCHO GRANDE, NORTH-CENTRAL VENEZUELA.

15.

Notes on *Ergasilus* Parasites from the New Brunswick, New Jersey, Area, with a Check List of All Species and Hosts East of the Mississippi River.

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INTRODUCTION.

The members of the genus *Ergasilus* represent the most undifferentiated of all the copepod parasites and clearly show a possible line of evolution from the free-living forms to the very specialized parasites that are to be found in other families and genera. Even in the genus itself one finds the transition taking place, and *E. chautauquaënsis* (which has never been found as a parasite) to *E. elegans,* which is parasitic only after the eggs begin to develop, and on to the other forms where the females are parasitic after they have become sexually mature.

The main characteristics of the genus are its cyclops-like appearance; 2nd pair of antennae enlarged and prehensile, 1st antennae six-jointed; first thoracic segment and head fused to form a large carapace; five pairs of swimming legs; the first four biramose, the fifth pair very degenerate and uniramose. Egg sacs are similar to those in *Cyclops*. The genus is typically fresh-water, though some ergasilids are to be found in brackish and marine waters. The type species of the genus is a very common European species, *E. sieboldi,* established by Nordmann in 1832.

These parasites are generally found clinging to the gill filaments, but one species, *E. megaceros,* has been found in the nasal fossae of the Fulton cat, *Ictalurus anguilla,* and another, *E. elongatus,* has been found attached to the bony gill rakers of the spoonbill cat, *Polyodon spathula.* At the present time they have been found to infest all of the major groups of fresh-water fishes and it is likely that no species of fresh-water fish is entirely free from the possibility of becoming a host. As far as is known, fishes are the only hosts on which this genus has ever been found. (See Mueller, 1936; Tidd & Bangham, 1945; Wilson, 1911, 1916, 1925, 1932; Wright, 1844.)

The males of *Ergasilus* are free-swimming throughout their lives. They are small and easily overlooked in plankton samples and consequently few of them have ever been described. The chief distinguishing characteristics in the males are the powerful maxillipeds, which are lacking in the females, and the small, weak second antennae.

The females are free-swimming during their early developmental stages and only attach themselves after mating. It is generally concluded (Wilson, 1911) that mating takes place only once while the female is still free-swimming. The sperms are stored in the semen receptacle and fertilize the eggs as they pass out into the ovi-sacs.

The breeding season apparently extends throughout the summer months. The length will vary from season to season, or from one region to another, depending on favorable water temperatures. In this area females were observed with fully extended egg strings on March 31. In the laboratory the incubation period was found to be around eight weeks, which is about the period of time observed by Wilson ("eight to nine weeks"). Henderson (1926) in her paper on *E. lucionercarium* from Canada, stated that it is likely that the females carry their egg strings throughout the winter. This is not the case in Westons Mills Reservoir, but it may be that in Canada, where the summer season is considerably shorter, the last batch of eggs does not get the chance to develop before cold water temperatures come and consequently must be carried over until the warmer temperatures of spring. In New Brunswick the breeding season is over by the middle of November.

OBSERVATION ON EPIDEMIC OF *Ergasilus* ON FISHES IN THE WESTONS MILLS RESERVOIR, NEW BRUNSWICK, N. J.

During the latter part of November, 1947, fishermen began to notice large numbers of fish dying in Westons Mills, a reservoir from which New Brunswick obtains its water supply. Local residents estimated that the fish were dying by the "thousands," and indeed the number of dying fish was so great

[1] The author wishes to express his appreciation to Mr. Herbert Groat, who first called attention to the epidemic; Dr. R. F. Nigrelli for assistance in making this paper ready for publication; and to Herbert Treuting and others who gave assistance when it was needed.

as to attract large flocks of sea gulls from the nearby Raritan River. The fish affected were apparently only two species, calico bass, *Pomoxis sparoides*, and bluegill, *Lepomis macrochirus*.

Some of these fish were brought to the Rutgers University Zoological Laboratory where they were examined for possible parasitic infestations. No intestinal parasites were found in excessive numbers nor did there appear to be any injury of body tissues, either external or internal. The gills appeared to be covered with an unusually heavy coating of mucus and microscopic examination revealed great numbers of copepod parasites of the genus *Ergasilus*. The blue color of these organisms, the three knobs on the inner edge of the second antennae towards the distal end, and the fact that they were all found in between the gill filaments seemed to indicate conclusively that these were of the species *caeruleus*. The hairs and spines on the appendages, along with other general morphological characteristics, were not quite in accord with Wilson's *caeruleus*, but there seemed to be a considerable amount of variation in this genus, depending on geographic location (Mueller, 1936). Wilson (1911) considers *caeruleus* a parasite of the vegetative Centrarchidae, and gives the explanation that the copepods on these fishes must locate themselves between the gill filaments to escape the discomfort and irritation to their gills from bits of vegetation.

A number of trips were made to the reservoir to collect fish during this period. Oxygen determinations were made at all depths and at no time was the O_2 concentration less than 10 ppm. Most of the fish were alive when captured. They could easily be spotted as they swam feebly on their sides on the surface of the pond. It was possible to come up alongside these fish in a boat and pick them up by hand. Occasionally a fish would sound on approach, but only to rise slowly to the surface after a short interval. On the first of such trips about a dozen fish were collected and taken back to the laboratory. These were placed in a well-aerated aquarium. At first they seemed almost dead—all lying motionless on their sides, with only an occasional movement of a fin. The next day, however, they seemed fully recovered and all were swimming about apparently quite normal. A few of these examined at this time were found to have a very heavy infestation.

In brief, the meager facts obtained on the epidemic from Nov. 27 to Dec. 10, 1947, can be summarized as follows:

1. Many calico bass and bluegills died during this period. No official estimates could be obtained, but laymen who observed the phenomenon estimated the deaths to be in the thousands.
2. One calico bass died for every ten bluegills. These were apparently the only fish affected.
3. All fish that were infested by these parasites appeared to have a heavy coating of mucus over the gills.
4. Estimated number of parasites on each fish was 250-300.
5. Age group (as determined by scale readings) was 1-2 years.

During the late fall of 1948 these observations were continued. A large fish trap was constructed and set in deep water as soon as ice covered the reservoir. All of the species of the Centrarchidae as well as one yellow perch were examined. Later in the year the fish were obtained by seining and from fishermen.

In this survey the large-mouth bass, *Micropterus dolomieu*, was found to be parasitized by a second species, *E. centrarchidarum*. This species is generally larger, broader, and found on the outside of the gill filaments, in contrast to *caeruleus* which is found between the gill filaments. In addition, there are no knobs on the inside surface of the distal end of the second pair of antennae.

Again there were morphological differences from Wilson's description of *centrarchidarum* and this phase of the work will be discussed in a later paper. Both species had the blue pigment but *centrarchidarum* was never as deeply pigmented as *caeruleus*. Strangely enough, both species had the same hair and spine formula on their appendages. This is: 1st exopod, I-0; 0-1; II-5, endopod 0-0; 0-1; II-3: 2nd exopod, 0-0; 0-1; 0-6, endopod, 0-1; 0-2; I-4: 3rd exopod, 0-0; 0-1; 0-6, endopod, 0-1; 0-2; I-4: 4th exopod, 0-0; 0-5, endopod, 0-1; 0-2; I-3.

In addition to the sampling of fish from Westons Mills, two other bodies of water in the New Brunswick area were sampled. These included the lower section of the Delaware-Raritan Canal and the small pond in Johnson's Park. The bluegills and calico bass in Johnson's Park were found to be free of ergasilids but the canal proved as fruitful as the reservoir. A summary of the fish examined is given in Table I.

Some interesting facts are foreshadowed in Table I. Although the amount of sampling from both bodies of water was not extensive enough to reveal fully the actual condition, nevertheless the methods by which these fish were obtained and the period of time over which the sampling was made certainly indicate the trend that one might expect to find if a more extensive sampling were to be taken.

For example, only five large-mouth bass were obtained—but under totally different conditions and at various times. The fact that all five had infestations does not indicate that all the bass are parasitized, yet one would expect to find a high percentage of the bass serving as hosts to these parasites. On the other hand, not once during this entire period of research has there ever been found a pumpkinseed infested with these copepods. Certainly one can say that for this species the incidence of parasitism is very low.

Again, viewing the information in the same light, one should expect the bluegills to be parasitized about 50% of the time in

TABLE I.

Result of the Samplings from Westons Mills and Delaware-Raritan Canal from Nov. 30, 1948-July 30, 1949.

Name	*Total No. Caught*	*Percent of parasitism*	*Average Length*	*Length Range*
Calico bass*	5	100%	5.79"	4"–7"
Bluegills	15	60%	5"	2"–7¾"
Pumpkinseed	6	0%	4"	3"–5"
Large-mouth bass	5	100%	6.4"	2½"–12"
Yellow perch	1	0%	7"	7"

* The highest infestation noted was on one calico bass 5¾" in length; 259 *caeruleus* were counted on this fish.

Westons Mills and the Canal. No data on calico bass could be obtained from the Canal but from the available information it would seem that these fish have become the most heavily infested in Westons Mills, not only in number of individuals but in number of parasites per fish. This is significant, for although the calico bass was found to be the most heavily infested as well as the most commonly parasitized fish, the epidemic of 1947 killed only one calico bass to ten bluegills. Unfortunately, here also, too little information is at hand. On the basis of the present data, however, there seems to be two logical explanations for this:

1. The calico bass are more resistant to the infestation of these gill parasites than are the bluegills and have been able to build up a resistance.
2. All the bluegills left are those that have built up a resistance to these parasites, or those that were only slightly parasitized.

Both fish are to be found in the same general type of environment and both have similar food habits, so apparently these two factors may be discounted.

Pathogenesis.

There has been a great deal of controversy over the extent of damage done by the ergasilids, as well as exactly what kind is done. Wilson (1911) states that "Living as they do upon the fish's gills, there can be but little doubt that they feed upon blood." Halisch (1939) in his observations on *E. sieboldi* and *E. minor* on the gills of tench states that extra-intestinal digestion is important and that much more tissue is destroyed than is ingested by the parasitic copepod. Blood may be taken in. Fungi may grow in the lesions.

In contrast to these two observations, Henderson (1926), in her work on *E. luciopercarium,* observed that "The gills may be heavily attacked without affecting the health of the fish. It is a harmless parasite, which, while it only benefits the unbidden guests, causes no lesions and consequently does no injury to the host." (If this is the case it should not even be called a parasite, but a commensal). She goes on to explain how, in her opinion, it is impossible for the parasites to injure the gill tissue, since the mouth parts of these organisms are too weak to pierce the gill tissue.

One might suspect that the claw-like, prehensile, second pair of antennae of the parasite is capable of at least some damage to the gill lamellae, although the mouth parts may be too small to cause any injury. However, the observations in the present studies showed no evidence of mechanical injury; neither was there any evidence of digested gill tissue or blood in the intestine of the numerous copepods examined, even in females with ovaries full of developing eggs.

We agree with Henderson (1926) that these parasites in all probability feed on the excessive mucus produced under the condition of the parasitism, or the many minute mucus or bits of organic debris and bacteria in this viscid material. However, it is altogether possible that the parasites may feed on sera, straining out the corpuscles.

A close examination of the mouth parts of these ergasilids will reveal the mandibles and second maxillae heavily fringed with setae. These would seem ideal for feeding on mucus or bits of organic debris and bacteria but hardly suitable for feeding on blood. Any pathological conditions of the gills may cause the mucus glands to secrete an excessive amount of mucus (Nigrelli, 1949). This has been especially apparent during infestations of trematode gill parasites. This condition has also been observed on many of the fish that were infested with these copepods[2]. It may be that an excess mucus secretion over the surface of the gills may lower the efficiency of the gills to absorb the dissolved oxygen in the water. Under normal water conditions when there is sufficient oxygen and all the chemical and physiological factors are in proper balance, this may not have any deleterious effects. However, if, for example, a factor such as the CO_2 concentration in the water should be increased, it might be sufficient to reduce the efficiency of the gills in absorbing the dissolved oxygen and so cause the fish to die of suffocation.

The highest death rate has been found among the younger fishes and it is the

[2] It must be kept in mind that the heavy coating of mucus which seems to accompany fish that are heavily infested with this parasite does not mean too much in itself. Fish that have been placed in preservative or that have died from other causes may show the same condition. Moreover, some fish that were heavily infested did not have an excess of mucus covering the gills. In such cases these fish exhibited no symptoms whatsoever and appeared perfectly normal. Apparently, there is a physiological balance here that is very delicately adjusted and which can be thrown out of balance only under certain specific conditions.

TABLE II.

Check List of the *Ergasilus* Found East of the Mississippi River.

Names and Synonyms	*Hosts*	*Localities Studied*	*Remarks*
E. caeruleus Wilson Synonyms: *E. confuscus* Bere *E. skryabini* Mueller	Yellow perch Trout perch Wall-eyed pike Gray pike, Blue pike Rock bass, Calico bass White bass Warmouth bass Crappie Green sunfish Blue-spotted sunfish Pumpkinseed Bluegill Lake trout Cisco, White fish Sucker, Long-nosed gar	Lake Mendota Trout Lake region Lakes Erie & Michigan Oneida Lake Mississippi River, Iowa	
E. centrarchidarum Wright	Rock bass, Calico bass, Large-mouth bass, Small-mouth bass, White bass, Warmouth bass, Green sunfish, Bluegill, Crappie, Pumpkinseed, Sunfish (?) Wall-eyed pike, Gray pike, Sauger, Silversides, Smelt, *Microgadus tomcod*	Lake Erie Lake Michigan St. Lawrence River Watershed Lake Champlain Black Lake, N. Y. Lakes St. John & Chibogamo, Quebec St. Andrew's Bay, N. B. Lake Maxinkuckee, Ind. Mississippi River, Iowa Clewiston, Fla. Woods Hole	
E. chautauquaënsis Fellows		Lake Champlain Lake Mendota Fairport, Iowa	Has never been found as a parasite, but may be like *elegans*
E. cotti Kellicot	Rainbow darter Sculpin—*Cottus bairdii*	Lake Erie Westerville, Ohio	
E. elegans Wilson	*Ameiurus* sp. Northern black bullhead Channel catfish Short-nosed gar Long-nosed gar	Lake Okeechobee Myakka River & Canals Peace River, Fla. Mississippi River, Ia.,	Parasitic only after eggs begin developing
E. elongatus Wilson	Spoonbill cat	Mississippi River, Iowa and Illinois	
E. funduli Krøyer	*Fundulus ocellaris*	New Orleans	Salt and brackish water
E. labracis Krøyer	Striped bass	Woods Hole Baltimore	Marine
E. lanceolatus Wilson	Gizzard shad	Cumberland River, Ky.	
E. lizae Krøyer	Common killifish Gulf killifish Broad killifish Striped mullet White mullet	Englewood, Fla. New Orleans	Salt and brackish waters
E. luciopercarum Henderson	Pike perches	Lake St. John Lake Chibogamo, Que.	
E. manicatus Wilson	Silversides Smelt Two-spined stickleback Top minnow (*Gambusia holbrooki*) *Jordanella floridae*	Englewood St. Andrew's Bay, N. B. Woods Hole Along Atlantic Coast	Marine

Names and Synonyms	*Hosts*	*Localities Studied*	*Remarks*
E. megaceros Wilson Synonym: *E. fragilis* Mueller	Fulton cat Fall fish	Oneida Lake, N. Y. Mississippi River, Iowa	Found in the nasal fossae and spiracles
E. mugilis Vogt	Striped mullet	Beaufort, N. C.	Marine
E. nigratus Wilson	Large-mouth bass	Mississippi River, Iowa	
E. osburni Tidd & Bangham	Burbot	North Central States	
E. versicolor Wilson Synonym: *E. celestis* Mueller	Fulton cat Red-mouthed buffalo fish Channel cat Common brown bullhead Mudcat Skip jack Yellow cat Eel cat	Mississippi River, Iowa Florida Lake Erie Lake Maxinkuckee	

younger fishes that would require the greatest amount of oxygen (in proportion to the gill area), due to their greater metabolic activity. At the same time it is the younger fishes that are more susceptible to attacks from disease and parasites since they are using all their available energy toward growth. Wilson states that it is the young fish that are most heavily parasitized and this is probably true—especially during an epidemic. However, larger fish may also be quite heavily parasitized. (See Table I).

The ergasilids on the large-mouth bass were never very abundant—never more than thirty on any individual. Although Wilson (1916) mentions fish fatalities from the ergasilids he does not mention which species of copepod causes death, nor which species of fish are killed. In checking all the literature on *centrarchidarum,* never were their numbers found to be as great as for *caeruleus.* Therefore, one wonders if *caeruleus* is not the only one that may appear in such numbers as to bring about the death of a fish.

This leads us to speculate on how many ergasilids must be present on a fish to cause death. It would seem that numbers that lead to the death of a fish at one time, appear to have no effect at another. However, during the epidemic of 1947 none of the dead fish had less than an estimated 250 copepods. Whether fewer parasites can bring about the death of a fish remains to be determined by further study.

It is apparent from the literature that *E. centrarchidarum* is the most widespread parasite and probably the best known. It has been found in all the main regions studied, including the marine habitat, but it has not been found on as many hosts (16) as has *caeruleus* (19), nor on as great a variety.

Caeruleus has not been found in all the areas that have been studied and so far has proved to be an exclusively fresh-water parasite. Additional research may also reveal that *caeruleus* is more widespread than *centrarchidarum.* It is unfortunate that most of the workers in this field have failed to make clear whether *caeruleus* has always been found between the gill filaments of its host. If it is found between the gill filaments of such clear-water fishes as the lake trout, cisco and white fish, certainly Wilson's explanation for their being found between the gill filaments is not substantiated.

E. versicolor is apparently third in abundance and seems to be more specific in its parasitism.

Many of the *Ergasilus* have only been found on one or a few hosts, but it is still too early to state definitely that they are specific for only those hosts.

Conclusions.

1. It seems quite likely that *Ergasilus* may indirectly cause death to fish, although it probably seldom causes extensive damage to any given fish population.
2. Young fish (1-2 years) are apparently the only ones on which these parasites may prove fatal. Although infestations have been found to be equally high on all age groups, more young fish appear to be heavily infested than older ones.
3. Ponds where the fish are overcrowded or that are small in area seem to be the only places where infestations become high enough to cause death.
4. Ergasilids do not feed on blood, but probably on mucus or bits of organic matter found in the viscid material.
5. Death of fish is probably due to a delicate physiological imbalance affecting the diffusion of oxygen through the gill tissues.

6. *E. caeruleus* can always be distinguished from *E. centrarchidarum* by the three knobs on the second pair of antennae, and by the fact that it is always found in between the gill filaments. Variations among these copepods are exceedingly great.
7. Although Wilson considers *E. caeruleus* a parasite of the plant-eating Centrarchidae, it is also found on species that are quite carnivorous and not generally found among aquatic vegetation. It undoubtedly is found most commonly on fishes that typically inhabit an environment of aquatic vegetation, such as the bluegill and calico bass.
8. Though *centrarchidarum* and *caeruleus* have often been found on the same fish (Wilson, 1911, 16), they were never observed together in the New Brunswick area nor was *centrarchidarum* ever observed on either bluegills or calico bass in this area. Neither was observed on any but the above species of fish.
9. It may be that certain factors, chemical, physical, physiological and environmental, or a combination of these, determine which hosts may be parasitized.
10. No reason could be found to explain why the pumpkinseed, *Lepomis gibbosus*, is free from these copepod parasites in this region.

Summary.

An epizootic in Westons Mills Reservoir which caused the death of many bluegills and calico bass was investigated.

A copepod parasite, *Ergasilus caeruleus*, was believed to be the indirect cause of the death of these fish. Apparently, metabolic wastes from the copepod or irritation to the gill tissues causes an excessive secretion of mucus. This mucus may lower the efficiency of the gills, so that when certain other factors are not in proper balance the fish will suffocate.

Large-mouth bass were found to be infested with another species *E. centrarchidarum*.

A brief survey of two other bodies of water in the New Brunswick area revealed that the incidence of parasitism from these ergasilids is quite high for bluegills, calico bass and large-mouth bass, but does not seem to be present on the pumpkinseed.

References.

Halisch, J.

1939. Anatomie und Biologie von *Ergasilus minor*. *Zeitschr. Parasitenk.*, 11 (2/3): 284-330.

Henderson, Jean T.

1926. Description of a Copepod Gill Parasite of Pike Perches in Lakes of Northern Quebec, Including an Account of the Free-Swimming Male and Some Developmental Stages. *Contr. Canadian Biol. & Fish.*, N. S. 3 (7): 235-246.

Mueller, J. F.

1936. Notes on Some Parasitic Copepods and a Mite, Chiefly from Florida Fresh Water Fishes. *The American Midland Naturalist*, 17 (5): 807-815.

Nigrelli, Ross F.

1949. Notes from Lectures on Fish Diseases.

Tidd, W. M. & Bangham, R. V.

1945. A New Species of Parasitic Copepod, *Ergasilus osburni*, from the Burbot. *Trans. Amer. Micr. Soc.*, 44 (3): 225-227.

Wilson, C. B.

1911. North American Copepods Belonging to the Family Ergasilidae. *Proc. U. S. Nat. Mus.*, 39: 263-400.

1916. Copepod Parasites of Fresh-Water Fishes, and Their Economic Relations to Mussel Glochidia. *Bull. U. S. Fisheries*, 34: 331-374.

1924. New North American Parasitic Copepods, New Hosts, and Notes on Copepod Nomenclature. *Proc. U. S. Nat. Mus.*, 64: 1-22.

1932. Copepods of the Woods Hole Region, Massachusetts. *Bull. U. S. Nat. Mus.*, No. 158: 1-623.

Wright, R. R.

1884. Notes on American Parasitic Copepoda. *Proc. Canad. Inst.*, N. S. 1:243-254.

16.

An Analysis of Reproductive Behavior in the Mouthbreeding Cichlid Fish, *Tilapia macrocephala* (Bleeker).[1,2]

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(Plates I-III; Text-figures 1-10).

INTRODUCTION.

Teleosts of the family Cichlidae are noted for their elaborate patterns of courtship, mating and parental care, and for the readiness with which they breed in the restricted confines of the small aquarium. It is largely because of these attributes that cichlids have become the subjects of several extensive investigations of fish behavior. Outstanding among these studies are those of Breder (1934) on the blue acara, *Aequidens latifrons*; Noble and Curtis (1939), Peters (1941) and Seitz (1942) on the jewel fish, *Hemichromis bimaculatus*; Peters (1937) on the small Egyptian mouthbreeder, *Haplochromis multicolor;* and Seitz (1940) on a closely related mouthbreeder, *Astatotilapia strigigena.*

These students have investigated topics such as schooling, sex recognition, courtship, territory, social dominance, spawning, parental care, the stimuli causing the release of various innate responses and many other related items of behavior. In these studies, mating behavior has been described qualitatively and in varying degrees of detail. Although the reports in most cases have been based on a number of observed spawnings, the results are given in a generalized or "averaged" form and the only suggestion of variability in behavior is found in such broad phrases as "this *usually* happens," or "the *typical* mode of behavior is." Moreover, the "averaging" is often achieved by means of subjective impressions rather than in terms of a calibrated or objectively weighted evaluation of behavioral characteristics.

Variability is a fundamental characteristic of biological phenomena, a characteristic which always merits careful consideration in studies of animal behavior. It is the writer's belief that the study of teleost behavior cannot extend very far beyond the present descriptive stages unless and until methods of a more quantitative nature are employed. Students of mammalian psychology, and particularly of rodent behavior, have made excellent progress by utilizing quantitative procedures. The present study afforded an opportunity for testing the applicability of comparable techniques in the study of the reproductive behavior of fish.

The present report is concerned with the average behavior and the range of variability under constant aquarium conditions of a type which can be readily duplicated. In other investigations now in progress, the mating activities of brain-operated and hormone-treated animals will be compared to the norms obtained in the present report.

Nothing appears to be known concerning the mating behavior of *Tilapia macrocephala* in the wild state, and the present report is hardly intended as a substitute for such an investigation. Nevertheless, wherever the behavior of fishes has been studied both under field conditions and in captivity, agreement has been fairly good, as for example in the Centrarchidae. It is anticipated that the over-all picture obtained in this study should prove to be essentially similar to conditions prevailing in the natural state, and that differences if any would be expected only in some of the lesser details.

LITERATURE.

Information concerning the breeding habits of *Tilapia macrocephala* and of related species belonging to the same genus has been furnished for the most part by aquarium hobbyists and through cursory observations by field naturalists. It is realized that because aquarists' reports often fall below generally recognized standards of scientific accuracy, as might be expected considerable confusion exists in the literature concerning certain aspects of the breeding patterns of *Tilapia.* Some of these difficulties may no doubt be attributed to an improper identification of

[1] The experiments herein reported were supported by a grant from the Committee for Research in Problems of Sex, National Research Council.

[2] Mrs. Magda Schonwetter assisted in many of the observations. Drs. Frank A. Beach and Charles M. Breder made numerous helpful suggestions on the conduct of the observations and experiments. Dr. Myron Gordon helped solve the feeding problem. Dr. T. C. Schneirla, Mr. James W. Atz, Mrs. Marie Holz-Tucker and Mr. Christopher W. Coates read the manuscript and made innumerable constructive criticisms. The author gratefully acknowledges his indebtedness to these people and those past and present associates of the Department of Animal Behavior who in ways too numerous to mention made possible the completion of this study.

the species in question, since aquarists sometimes trust the knowledge and dependability of fish dealers for the identity of their subjects. Nevertheless it is possible to obtain from this literature a rough picture of the reproductive habits of the genus *Tilapia*. For these reasons the inclusion of numerous aquarists' accounts is considered expedient. What may be offered herein is by no means intended to be a comprehensive review of the extensive popular literature.

Brief descriptions of the breeding habits of *Tilapia macrocephala* can be found in the aquarium texts of Stoye (1935), Arnold and Ahl (1936) and Innes (1944). In addition, reports on the spawning of *Tilapia heudeloti* (which according to Boulenger (1915) may be a variety of *Tilapia macrocephala*) have been presented by Breder (1934) and Schoenfeld (1934). These accounts tell us briefly that (1) a nest is built by the mating pair; (2) the female deposits the eggs in the nest; (3) the male fertilizes the eggs as soon as they are deposited; (4) shortly thereafter the male takes the eggs into his mouth; and (5) the eggs hatch and develop in the mouth of the male. How long the eggs are retained in the male's buccal pouch is not indicated, but Stoye (1935) reports two cases where eggs were carried 24 to 29 days respectively. Stoye considers these periods abnormally long as a result of excessive disturbances.

With four probable exceptions, all the species of *Tilapia* whose spawning habits have been reported are mouthbreeders. The four exceptional species remove their larvae to sand pits in typical cichlid fashion. These non-mouthbreeding species are (1) *Tilapia guinasana* (Roloff, 1938, 1939), (2) *Tilapia spaarmanii* (Hey, 1945, 1947; Anon., 1948)[3], (3) *Tilapia melanopleura* (Svenssor, 1933; Bertram, Borley and Trewavas, 1942) and (4) *Tilapia zillii* (Bade, 1923; Stoye, 1935; Arnold and Ahl, 1936; Bertram, Borley and Trewavas, 1942). However, Liebman (1933) describes *Tilapia zillii* as a mouthbreeder. Incubation of the eggs is accomplished by the females of *Tilapia flavomarginata* (Pellagrin, 1906)[4], *Tilapia galilaea* (Pellegrin, 1903, 1905), *Tilapia martini* (Boulenger, 1906), *Tilapia microcephala*[5] (Junghans, 1918) and *Tilapia mossambica*[6] (Bade, 1923; Dietz, 1926; Roloff, 1937; Peters, 1937a, 1939; Seleuthner, 1941; Hey, 1947). The same appears to be true for *Tilapia squamipinnis*, *Tilapia lidole*, and *Tilapia shirana* (Bertram, Borley and Trewavas, 1942).

The male is credited with the care of the eggs in *Tilapia dolloi* (Asch, 1939), *Tilapia heudeloti* (Breder, 1934; Schoenfeld, 1934), *Tilapia macrocephala* (Stoye, 1935; Innes 1944), *Tilapia microcephala* (Schreitmüller, 1920) and *Tilapia simonis*[7] (Lortet, 1875; 1883). However, there is some disagreement on this point since both the male and female are believed to incubate the eggs in *Tilapia simonis* (Pellegrin, 1903; Liebman, 1933), *Tilapia galilaea* (Liebman, 1933), *Tilapia microcephala* (Locke, 1932), *Tilapia nilotica* (Boulenger, 1901) and *Tilapia zillii* (Liebman, 1933). Bodenheimer (1927) claims that females alone incubate the eggs of *Tilapia simonis*, and Arnold and Ahl (1936) claim the same for *Tilapia dolloi*.

Irvine (1947) states that the male or possibly both sexes of *Tilapia discolor* and *Tilapia heudeloti* incubate the eggs, but contrary to the findings of Boulenger, Irvine relegates this function to the female in *Tilapia nilotica*. Liebman (1933) believes that it is quite general in Palestine cichlids for both parents to incubate the eggs, but the number of females performing this function is higher than the number of males so doing.

The length of the incubatory period has been reported for only a few species. Arnold and Ahl (1936) say about 14 days for *Tilapia dolloi;* Schreitmüller (1920) gives 4 to 6 days for *Tilapia microcephala;* Roloff (1937) reports 21 days for *Tilapia mossambica;* Bade (1923) offers a value of 15 days while Dietz (1926) and Seleuthner (1941) both give 13 days as the incubatory period of this species.

The retrieving into the female's mouth of newly released young has been reported for *Tilapia dolloi* (Arnold and Ahl, 1936), *Tilapia macrocephala* (Stoye, 1935), and *Tilapia mossambica* (Roloff, 1937; Seleuthner, 1941) while in *Tilapia microcephala* the male is credited with that activity (Schreitmüller, 1920).

Nest making by these mouthbreeders has received some general attention. On a number of occasions, Lortet (1883) witnessed the female *Tilapia simonis* lay approximately 200 eggs in a small excavation which she had hollowed out and cleaned in the silt among the reeds. Nest building by both the male and the female *Tilapia nilotica* was observed in the field by C. L. Boulenger (1908). Roloff (1937) describes the nest of *Tilapia mossambica* as being 20 cm. in diameter. Seleuthner (1941) reports a nest for this species which was 25 cm. in diameter and reached a depth of 4 cm. in the middle, while Hey (1947) pictures it as a "small saucer-shaped depression." Bertram, Borley and Trewavas (1942) describe the nest of *Tilapia squamipinnis* as a circular depression.

Other mouthbreeding cichlids are listed by Peters (1937) as belonging to the genera *Astatotilapia*, *Ectodus*, *Geophogus*, *Hap-*

[3] Also recorded in "Report No. 1 (1944) Inland Fisheries Dept., Union of South Africa"—1945.

[4] Designated by Boulenger (1911) as *Tilapia andersonii*.

[5] *Tilapia microcephala* = *Tilapia heudeloti*. According to Boulenger (1915, p. 178) *Tilapia macrocephala*, and *Tilapia multifasciata* "may ultimately have to be regarded as varieties of *T. heudeloti*. I am unable to find characters by which to separate them sharply."

[6] *Tilapia mossambica* = *Tilapia natalensis*.

[7] Placed in the genus *Tilapia* by Boulenger (1899) but now referred to a new genus *Tristramella* by Trewavas (1942). Lortet (1875) called this fish *Chromis paterfamilias*.

lochromis, Pelmatochromis and *Tropheus*.[8] It is to be noted that at least some of these genera also contain non-mouthbreeding species, suggesting a multiple origin of this habit even within the cichlid family. This problem has been considered in some detail by Breder (1933) and Myers (1939).

The small Egyptian mouthbreeding cichlid, *Haplochromis multicolor*, and a closely related form, *Astatotilapia strigigena*, have been the most popular and intensively studied of all the mouthbreeding fish. In addition to the scientific investigations previously mentioned, more than 30 accounts of the spawnings of these two fish have appeared in the last three decades, the majority of them in the Wochenschrift für Aquarien-und Terrarienkunde. These accounts, which are relatively consistent in their general implications, demonstrate that the spawning behavior of these species differs considerably from that of the various species of *Tilapia* described above. For this reason what is known about the *Haplochromis* and *Astatotilapia* mating patterns is summarized briefly for the purposes of comparison.

In these species the male does practically all of the nest building. Upon the completion of the nest, the female starts the oviposition by depositing between four and ten eggs in the nest. The male immediately fertilizes the eggs after which they are picked up by the female. This cycle is then repeated as the female lays a second batch of eggs. Between five and ten such cycles have been reported by various authors as comprising a spawning. The eggs are carried for 9 to 20 days, after which the young are released. However, the young are taken back into the female's mouth at night and at other times when disturbed. Such a retrieving of the young has been the subject of a special investigation by Peters (1937).

Material and Methods.

Tilapia macrocephala (Bleeker) is native to West Africa, particularly in the region of the Gold Coast. Boulenger (1915) describes the species as coming from the Gold Coast, Ashantee and Lagos. Many of his specimens were taken from the Ancobra river and Secconda lagoon in the Gold Coast, and from the Lagos lagoon. According to Arnold and Ahl (1936) the fish is found in the brackish lagoons of the coast and the swampy deltas of rivers.

The individuals utilized in this study were selected from a laboratory-bred stock which had been maintained for a number of years prior to the start of the present research.[9] Males were chosen for the brightness of their yellow operculum which is a secondary sex character (Pl. I, Fig. 1). The females (Pl. I, Fig. 2) were selected on the basis of the complementary sex character, namely a deep red spot in the center of the gill cover.[10] These dimorphic color patterns appear at sexual maturity and disappear after castration (Aronson, in manuscript).

Pairs were established by random selection and were placed in 54-liter aquaria, 60 cm. × 30 cm. × 30 cm. each containing roughly 36 liters of water. The side and rear walls of these tanks were painted pale blue to minimize any possible disturbing influences from neighboring tanks, and also to facilitate the ability of the investigator to follow the activities of the fish. The tanks were located in a greenhouse the temperature of which was maintained throughout the year at 26° C. with a positive and negative variation of approximately 3° C. To furnish hide-outs for the fish which at the same time would not obstruct the observer's view, a mat of floating plants was placed in every tank. *Cabomba* was extensively used for this purpose, but *Sagittaria subulata* was found to be somewhat more suitable and was used whenever available.[11] The fish were fed mostly a dehydrated preparation consisting of dried shrimp, oatmeal, beef liver, lettuce and spinach. At times this was supplemented by live tubifex worms. Occasionally the fish nibbled at the stonewort *Nitella*, and this was placed in the tanks when available. The tanks were aerated continuously, and the water was changed whenever it became excessively murky. This was approximately once a month. Tap water brought to the proper temperature was used in washing the tanks and for replacement.

In order to avoid injury to the fish due to excessive nipping which often occurred after spawning, a transparent glass partition was placed in the aquarium, separating the male from the female as soon as observations of oviposition were completed. As the individual carrying the eggs (generally the male) eats little or nothing during the incubatory period, brooding fish were not fed during this interval. By the time that the young were released from the male's mouth, the females often were prepared to spawn again. However preliminary observations indicated that when such spawnings occurred males sometimes behaved abnormally, due apparently to the protracted period of inanition. To avoid this difficulty an arbitrary rule was established to the effect that males were separated by a transparent glass partition from females for one week after they had released their young or had swallowed their eggs. This interval allowed the males to feed and regain their strength. While thus iso-

[8] An older listing of mouthbreeding cichlids given by Pellegrin (1903) includes the genera *Geophagus, Acara, Chaetobranchus, Tilapia, Paratilapia, Pelmatochromis, Ectodus* and *Tropheus*.

[9] I am greatly indebted to Miss Ethelwyn Trewavas of the British Museum for kindly checking and verifying the taxonomic identity of the fish as *Tilapia macrocephala*.

[10] Examination of this spot by Aronson and Holz-Tucker (in manuscript) has revealed that it is in actuality a semi-transparent window through which the underlying red gill can be seen.

[11] The author wishes to express his appreciation to Dr. Myron Gordon of the New York Zoological Society for furnishing all of the sagittaria used.

lated, females often spawned alone but observations showed that a considerable amount of courtship took place through the glass partition.

To prevent the parents from eating their young after they were released, large masses of the stonewort *Nitella* were placed in all tanks where young were being incubated. The stonewort was distributed equally on both sides of the partition since the newly released fry could easily swim through the cracks at the intersection of the partition and the glass walls of the tank. Disturbances caused the young to swim into the fine interstices of the *Nitella* where they would not be followed by their cannibalistic parents.[12]

The criteria employed to indicate the approach of oviposition were (1) persistent nest building, mostly by the female, (2) heightened courtship activity, and (3) protruding genital tubes. When these signs were observed, continuous records were taken of the courtship and mating activities of the pair up to the time of spawning and for one-half hour thereafter. Attempts were made to secure continuous pre-spawning records for three hours. However, this goal was attained in only a small number of cases with the result that the records vary from just a few minutes before spawning up to the full three-hour span. A serious difficulty was encountered here in that the activities of many promising pairs were observed continuously for many hours up to a whole day without the fish ever ovipositing.

After the present experiment had been terminated, behavior during the interspawning interval was studied, using different pairs of *Tilapia*. The experimental conditions were the same as before with the following minor exceptions: (1) no plants were used but instead inside aquarium filters served as hide-outs; (2) the water in the tanks was never changed; (3) the males were never separated from the females. The actual spawnings of these pairs were not witnessed, all ovipositions being recorded as having occurred at the time the eggs were discovered in the male's mouth. All pairs were checked twice daily for eggs. A 15-minute record of the behavior of a given pair was taken 5 or 6 days after the spawning and again on the 15th or 16th day. The interval between successive spawnings varies from 8 days up to almost a year with a mode of 15 days (Aronson, 1945). Approximately two-thirds of the intervals are less than 29 days. Thus the 5- or 6-day score serves as an intermediate record for the shorter interspawning intervals, while the 15- or 16-day score serves in the same capacity for the longer intervals. Obviously some of the 15-day records could not be taken because of intervening ovipositions. Many of these observations served, moreover, as behavior records for varying days before spawning.

Qualitative Description of Reproductive Behavior.

In order to furnish the reader with the proper background for the quantitative investigation, it is appropriate to present first a general description of mating activities. This account does not take into consideration the question of the range of variability and any exceptional items of behavior. Details concerning many of the generalizations made here will be considered in the next section.

Certain of the behavioral patterns which increase in their frequency of occurrence prior to spawning and which lead up to the acts of oviposition and fertilization generally are classified as courtship activity. Such behavior appears to express the level of sexual excitability of the given individual. In accordance with the views of Huxley (1914, 1938), Howard (1929) and Marshall (1936), it is assumed that courtship tends to hold the pair together, and through mutual stimulation may lead to a well synchronized spawning. In the terms of Schneirla's (1946) discussion, such relationship may be thought of as involving trophallactic processes, and the temporal aspects of these interactivities are of significance from the standpoint of adaptive function. *Tilapia* eggs (Pl. I, Fig. 2; Pl. II, Figs. 3, 4), as well as those of other oviparous teleosts, are shed in a flaccid state, but rapidly become hard and turgid upon entering the water. That is, they "water harden" (Breder, 1943). Hence, to insure fertilization the male must deposit his sperm over the eggs within a very short time after they are laid. An adequate synchronization of the pair's reproductive processes thus appears to be critically important for effective species survival.

There follows a description of the early courtship behavior of *Tilapia macrocephala*: (1) The male and female approach each other and suddenly dip their heads; or one member of the pair lowers its head. This

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[12] This was the author's first experience with the maintenance of tropical fish. Since then, several innovations have been developed. Inside aquarium charcoal filters are now placed in every tank. These keep the water clean and eliminate the need for changing it. Plants are not used since they grow poorly in *Tilapia* aquaria. The food formulae have been modified as follows: (1) *Wet mash*: 2½ lbs. liver; ½ lb. chopped lettuce and spinach; ½ lb. dried ground shrimp (mostly shell); ½ lb. dried and ground refined shrimp (mostly muscle); Pablum (or other precooked infant cereal)—enough to make thick paste (approximately 3½ lbs.); 1 pinch salt. The liver is chopped, about 1 cup of water added, and the mixture is then liquefied in a blending machine. All ingredients are mixed together with sufficient Pablum to make a paste. The food is further solidified and preserved by packing into jars and immersing them in boiling water for about 10 minutes. (2) *Dry food*: 12 lbs. dried shrimp (mostly shell); 12 lbs. dried refined shrimp (mostly muscle); 10 lbs. liver; 6 lbs. chopped lettuce; 6 lbs. chopped spinach; 28 lbs. Pablum; 2 level teaspoons salt. The ground spinach and lettuce are mixed with the Pablum and cooked for 15 minutes. The liver is cut into slices and boiled for 15 minutes in a minimum amount of water and then chopped. All ingredients are mixed together and the resulting paste spread about ½ inch thick on trays. When almost completely dry, the food mixture is ground and sifted through screens of several coarsenesses.

The sexes are no longer separated after the spawning. If the fry are to be saved they are forcibly removed from the parents' mouths on the tenth day post-oviposition, and are placed in small aquaria. At this age the young do very well without further parental care, and thus, losses through cannibalism are easily avoided.

behavior has been termed "head-nodding." (2) When one member of the pair approaches the other, spreads its opercula and expands its buccal pouch, we have called this act a "throat-puff." (3) The male or female ceases swimming movements and the trunk musculature appears to quiver for a fraction of a second. We have named this a "body-quiver." (4) When one member of the pair slaps the other with its tail, this has been called a "tail-slap." Included in this category were the frequent cases where tail-slapping motions were quite distinct, but where actual contact with the partner was not made.

Closely associated with the courtship acts, but displayed as well in many pairs throughout the interspawning interval, is a mode of behavior which we have termed "nipping." This occurs when a fish swims after its partner, and then with a sudden dart nips or bites the body of its mate. Nipping also occurred at times without a previous chase. Sometimes the male and female may nip each other simultaneously and occasionally they may even lock jaws. Frequently observed cases in which the pursuing fish darts ahead but misses the fleeing opponent also have been included under the general heading of nipping.

In addition to its association with courtship and spawning, nipping behavior appears to be related to the establishment of social hierarchies and the formation of territories. These further relations of nipping have not as yet been investigated.

The above-mentioned patterns of behavior usually appear as quite distinct, but occasionally they tend to merge into one another, so that discretion on the part of the observer is often called for in assigning a particular courtship act to its proper category. Oftentimes two or more courtship acts may be displayed in rapid succession, a frequent combination being a head-nod, throat-puff and body-quiver. Another commonly occurring combination is the throat-puff and tail-slap.

Readers acquainted with the courtship behavior of other cichlid fishes will readily recognize the resemblance of the *Tilapia* pattern with those of other cichlids. Reactions such as the body-quiver, the throat-puff and the tail-slap in some form seem to be prevalent throughout the family.

Nest-building is first observed after intensive courtship has been in progress for several hours or days. Most of this activity is conducted by the female who begins scooping up mouthfuls of gravel from scattered locations in the bottom of the tank. Soon the excavating is confined to one location, and the construction of a nest begins. Often two or more nests are constructed prior to the spawning, and sometimes nests are built and then destroyed during the construction of an adjoining nest. The nests are most often round or slightly oval. If the gravel substratum of the aquarium is not too thick, the fish dig down to the slate bottom of the tank. If, however, the depth of the gravel is more than 2 or 3 cm., the nests do not reach the slate.

In our study the length of time taken to complete a nest varied considerably from as little as one-half hour up to what appeared to be several days. In the latter case, the nest-building activity occurred in spurts, followed by periods of quiescence. The rapid builders generally worked continuously until the nest was completed. A small amount of nest-building was accomplished by sweeping movements of the tail and pectoral fins. However, this has been interpreted as incidental to swimming and balancing movements and not directly related to nest building.

After the nest is more or less completed, nest-building decreases considerably and is supplanted to some extent by nest-cleaning (Pl. I, Fig. 1) in which the female, and occasionally the male, pick continuously at the bottom of the nest. Nest-building and nest-cleaning are always interspersed among various phases of courtship responses.

As the nest takes form, the genital tubes of the male and female become more prominent. At this time, the male begins to swim slowly over the nest, rubbing his genital tube over the bottom. We have called this "passing-nest." Later when the female completes the nest, she likewise "passes-nest." Thus the pair circle around and around, rubbing their genital tubes over the nest. This behavior is often interrupted by periods of courtship, nest-building and nest-cleaning activity. As soon as a fish starts passing-nest, the genital tubes become fully erected, but if this activity ceases for a time, the tubes generally recede somewhat. This suggests that mechanical stimulation is one factor causing the erection of the genital tube. Since fish not on the verge of spawning are sometimes seen with partially extended genital tubes, other stimuli seem to be involved in the partial erection of the genital tubes. Courtship activity and hormones are suggested as possible factors.

After the passing-nest behavior of the male and female has been in progress for some time, the female stops in the nest during a "pass-nest," and her body musculature quivers for a second or two. This has been called a "spawning-quiver." Males also exhibit spawning-quivers, but in the male these responses generally are less distinct and are seen less frequently.

Spawning-quivers were the final prespawning acts and indicated the imminence of the oviposition. During one of these quivers a batch of approximately 10 to 20 eggs is extruded by the female in what we have termed an "oviposition movement" (Pl. I, Fig. 2). The female then swims just past the nest. She is followed by the male who passes-nest, usually rubbing his genital tube over the newly laid eggs and sometimes exhibiting a spawning-quiver. This complementary act has been termed a "fertilization movement" (Pl. II, Fig. 3). Sperm

apparently are emitted at this time, although no male products were apparent in our observations. The female then repeats her oviposition movement which is followed closely by a second fertilization movement of the male. After two to four such egg-laying cycles, the female swims rapidly from the nest for a distance of 15 to 30 cm., then faces the nest. Meanwhile the male swims in the vicinity of the nest for a minute or so, then rapidly picks up the eggs with his mouth (Pl. II, Fig. 4; Pl. III, Fig. 5).

In our investigations there were a few exceptional cases where the male did not pick up the eggs. Then the female nipped and tail-slapped the male violently, exhibited some courtship behavior, and finally after 10 to 20 minutes of this activity she picked up the eggs and carried them in her mouth (Pl. III, Fig. 6). We found that at times, because of the unequal sizes of the male and female, all the eggs could not fit into the male's mouth, the female would pick up the remaining eggs, but not until 10 to 20 minutes had elapsed.

Post-spawning activity consists for the most part in poking around the nest, first by the male, and later by the female as well. If any of the eggs are missed when the original spawn was picked up, they are almost always recovered during this poking activity.

After several minutes, this poking behavior sometimes gives way to extensive nipping and mouthing in which one member of the pair, generally the female, soon dominates and the other retreats into hiding.

The eggs hatch in 5 days and are carried from 2 to 15 days further, during which time the embryos continue to develop. The young are released abruptly and most of them are sufficiently developed at this time to suggest that further parental care would not be advantageous to them. Parental care appears to end suddenly with the release of the young. In fact, parents sometimes eat their newly liberated offspring. Never did we see the young swim back into the parental mouth as has been described by some authors for this and other *Tilapia* species, and which is such a striking characteristic of the small Egyptian mouthbreeders, *Haplochromis multicolor* (Peters, 1937).

With this brief description of the mating pattern we turn now to an analysis of the actual counts made of the frequency of occurrence in relation to the time of spawning of many of the behavioral acts described above.

Analysis of the Mating Pattern.

For the purpose of analyzing the data, records were organized in the following manner. For each observed spawning, the time of appearance of the first batch of eggs was designated as the zero minute. The 15-minute period just prior to the zero minute was called the first pre-spawning interval. The period 15 minutes to 30 minutes prior to the zero minute was named the second pre-spawning interval. Twelve pre-spawning intervals were similarly measured. Again starting from the zero minute, the 15-minute interval which followed was called the first post-spawning interval, and a second post-spawning interval was likewise measured. The number of times that the various courtship and mating activities (tail-slaps, passing-nest, etc.) were recorded during each 15-minute pre- and post-spawning interval was determined for both the males and the females for all observed spawnings. With data assembled in this manner, a series of distributions was obtained (one of each behavior pattern of both the male and female for each interval). Almost all of these were strongly skewed to the right. The arithmetical mean obviously is a poor representation of the central tendency of a markedly skewed distribution. Medians are generally more suitable, but a better method of treating such data is to employ a transformation. In many cases by use of the transformation $X = \sqrt{x}$, binomial distributions were obtained which could be treated as normal curves.[13] These were checked by plotting cumulative distributions on arithmetic probability paper. However some of the distributions were not normalized following the above transformation, but approximated closely the Poisson series. This was particularly true with infrequently occurring items, where the highest frequency was zero and where the mean was considerably smaller than one. Theoretical Poisson distributions were calculated from Pearson's (1914) tables and the goodness of fit of the actual distributions was tested by the chi-square method.

Still other distributions did not approximate either the normal or Poisson series. As will be noted later, these were not subjected to further statistical analysis.

For the normal distributions, the means, range, theoretical range ($M \pm 3\sigma$), standard deviation and standard error of the mean were calculated. These were plotted graphically in a time sequence, using the method of comparing ranges and means developed by Dice and Leraas (1936) as modified by Simpson and Roe (1939). Since the length of the pre- and post-spawning records varied inadvertently for each spawning, the calculated means for each interval are based upon a varying number of spawnings. Simpson and Roe (1939) point out that the method of Dice and Leraas is less reliable when the frequencies and standard errors of the mean vary greatly. Therefore, in critical cases where the graphic method was suspected of being inaccurate, P values were calculated. The solid lines in Text-figs. 1-6, 8 and 9, indicate females; the broken lines males. The heavy vertical lines designate actual ranges of the distributions. The adjacent light vertical lines indicate theoretical ranges ($M \pm 3\sigma$). The large dots represent the means, while the short horizontal lines above and

[13] The writer wishes to acknowledge the aid given by Dr. Charles P. Winsor in suggesting the use of this transformation.

below the means indicate the range of M $\pm 2\sigma_M$. When these ranges overlap, it may generally be assumed that the differences between the means are not significant. Conversely, if M $\pm 2\sigma_M$ do not overlap, the differences between the means are significant. The limitation of this method has already been noted.

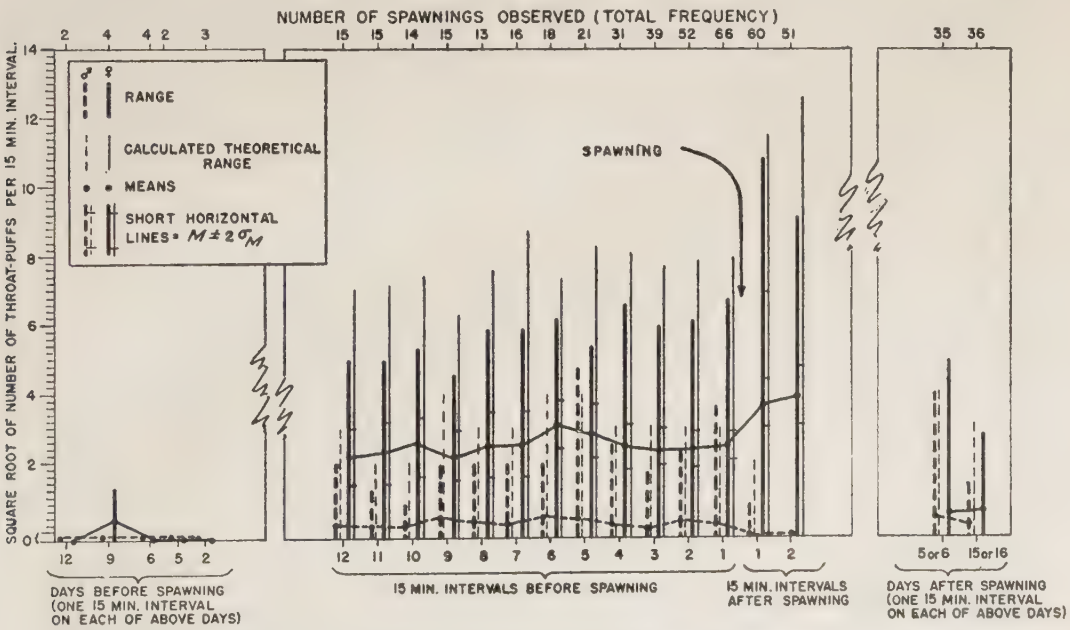
For the Poisson series, the theoretical ranges were considered to run from zero to that value of the variate having a relative frequency of .003 or less. Means were compared by the method described by Snedecor (1946). Because of the asymmetrical nature of the Poisson distribution the graphical method of comparing means described above cannot be used. Hence, in the following graphs, the range of M $\pm 2\sigma_M$ are not indicated for the Poisson distributions.

Where the distributions did not conform reasonably well to either a normal or Poisson series, only the means and actual ranges are presented on the graphs.

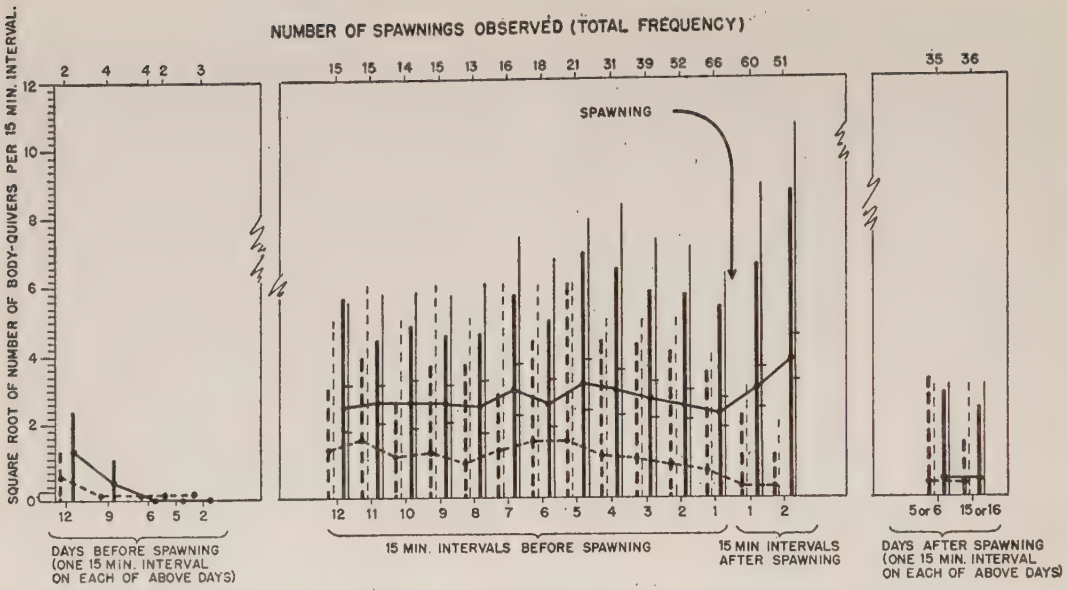
The 15-minute records on the 5th or 6th post-spawning day and on the 15th or 16th day were treated in a similar manner. Since a number of pairs spawned again within two weeks after these observations were made, it was possible to use some of these data as records of behavior on the 2nd, 5th, 6th, 9th and 12th pre-spawning days. Because of the small number of cases, only means and ranges are indicated graphically.

THROAT-PUFFS. As seen from the graph in Text-fig. 1, the females (solid lines) exhibited this behavior very rarely on the several days they were observed before the spawning. One female throat-puffed just once on the 9th pre-spawning day. However, by three hours before spawning, the throat-puffing frequency had reached a rather high level, which was maintained with little fluctuation right up to the spawning. Immediately after the egg laying, throat-puffing activity increased sharply. To be sure that this rise was not due to chance fluctuation, the means of the first pre- and post-spawning intervals were compared and were found to differ significantly ($P<.01$).

The males showed the throat-puffing behavior much less frequently than the females (Text-fig. 1, broken lines). On the several days the pairs were observed prior to the spawning, no throat-puffing by the males was seen. At three hours before the egg laying, a low frequency of throat-puffing was recorded, and this level was maintained up to the spawning. When these data were treated by utilizing the transformation $X = \sqrt{x}$ as already described, the frequencies of male throat-puffs were found to be distributed in a Poisson fashion with zero the highest frequency, an indication that the mean frequencies were less than one. This raised the question whether the males of just a few pairs were responsible for the bulk of the throat-puffing activity. A partial answer to this question was obtained by selecting the 25 spawnings in which continuous records for the first hour before spawning were available. It was found that during this hour, 64.0% of the males exhibited no throat-puffing at all. This contrasts with the figure of only 4.0% for the female. Similarly, in the seven pairs where continuous records for the first two pre-spawning hours were available, 57.1% of the males did not throat-puff. From this we may conclude that a consider-



TEXT-FIG. 1. Fluctuation in male and female throat-puffing behavior before and after spawning.



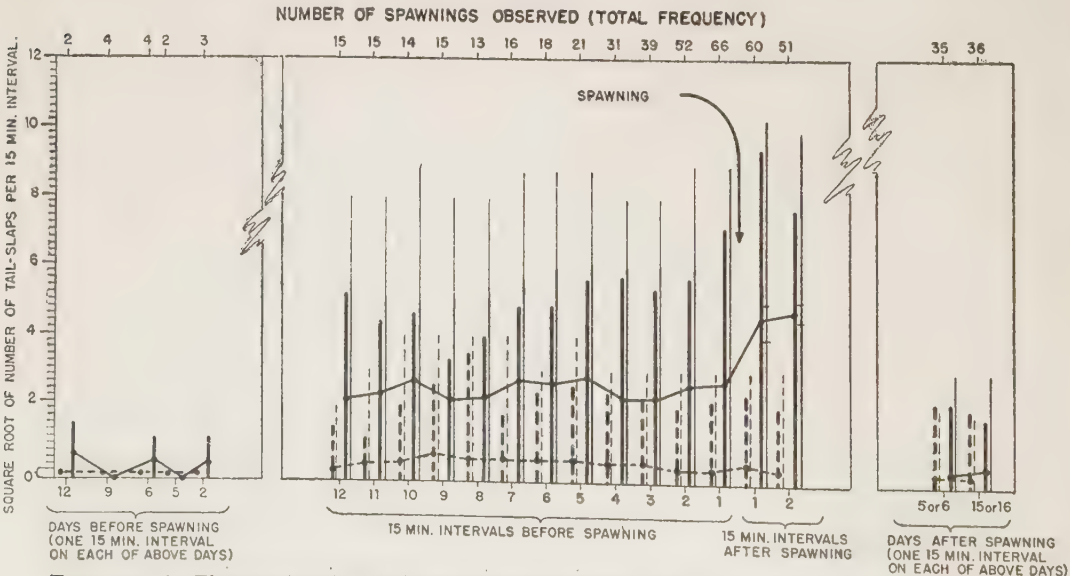
TEXT-FIG. 2. Fluctuation in male and female body-quivering behavior before and after spawning.

able number of males exhibited little or no throat-puffing behavior prior to the spawning.

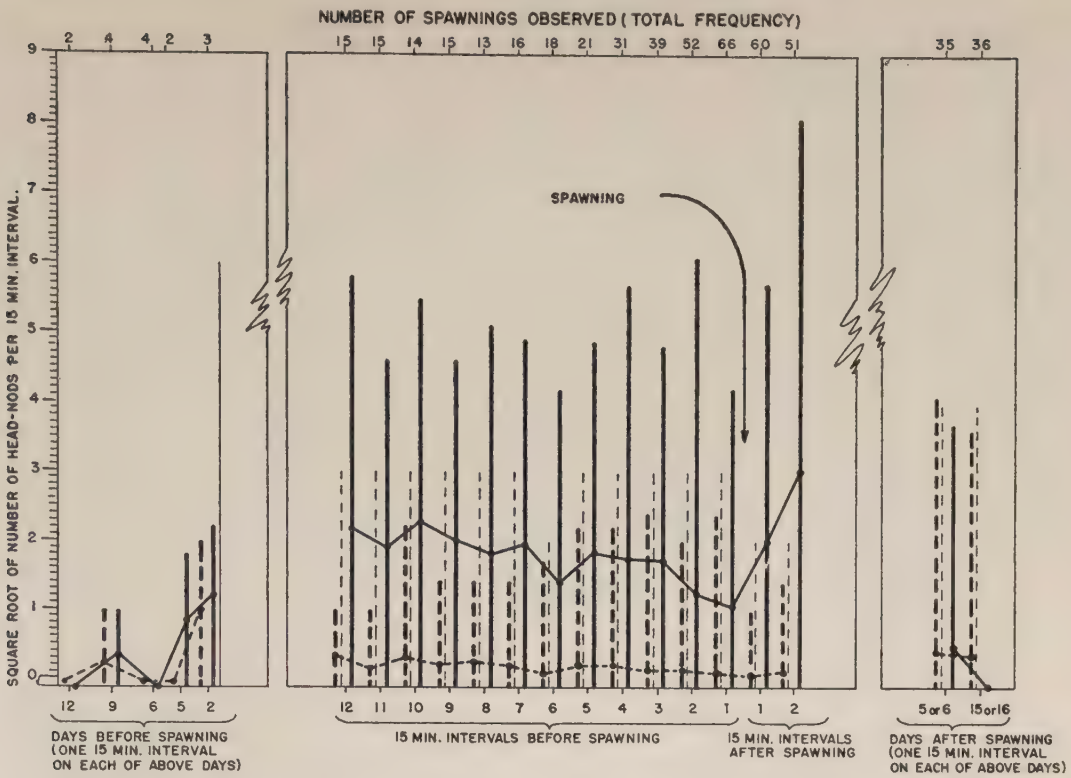
Immediately after the egg laying, throat-puffing by the male was no longer observed. Since the mouths of the males were now filled to capacity with eggs, it seems better to say that after the spawning throat-puffing could not readily be identified. By the 5th or 6th post-spawning day, many of the males were no longer carrying eggs, and now the throat-puffing behavior had reached the pre-spawning level.

BODY-QUIVERS. Only an occasional body-quiver was exhibited by the males and females on the several days they were observed prior to the spawning (Text-fig. 2), but by three hours before oviposition the body-quivers (solid lines) were very frequent occurrences in the female. They remained at this relatively constant level until the spawning, after which there was an abrupt rise. The means of female body-quivers for the first pre- and post-spawning intervals were compared, and the latter were found to be significantly higher ($P = .021$). At five days after spawning the females' body-quivering had dropped far below the immediate pre-spawning level, and remained the same during the observation period on the 15th or 16th day.

The body-quiver frequency of the males at



TEXT-FIG. 3. Fluctuation in male and female tail-slapping behavior before and after spawning.



TEXT-FIG. 4. Fluctuation in male and female head-nodding behavior before and after spawning.

three hours before spawning was considerably less than the females' and again these data were best treated as Poisson distributions. The behavior remained at this level until the fifth pre-spawning interval when it started to slope off, reaching a minimum at the first pre-spawning interval. However, when the male body-quivers of the fifth and first pre-spawning intervals were compared, this slope appears not to be significant ($P > .10$). On the 5th or 6th post-spawning day, and on the 15th or 16th post-spawning day, the body-quiver frequency of the males was very close to that of the females.

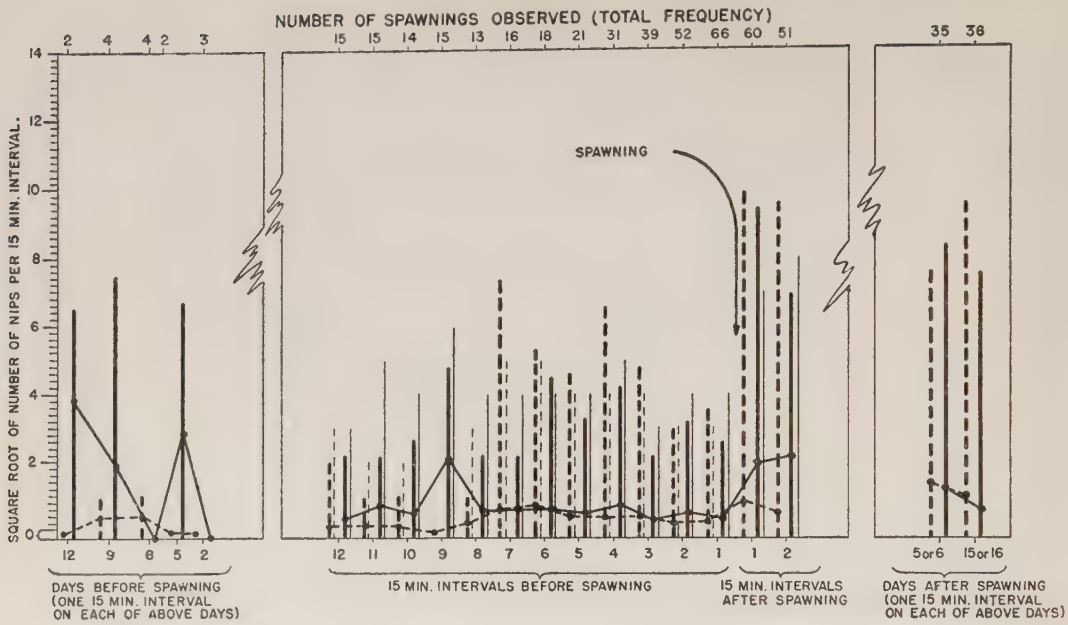
Of the 25 spawnings in which continuous records were available for one hour before the spawning, 100% of the females and 80.0% of the males exhibited body-quivering at least once. In the seven ovipositions in which continuous two-hour pre-spawning records were taken, 100% of the males gave body-quivers at least once. Thus while this courtship pattern is exhibited more frequently by the females, practically all males show some body-quivering activity prior to the egg laying.

TAIL-SLAPS. With the transformation previously described, the data of both the male and female were found to be distributed in a Poisson fashion, excepting the first two post-spawning intervals of the female which were normally distributed (Text-fig. 3). On the several days prior to the spawning occasional tail-slapping by the female was observed, but at three hours before the egg laying, the occurrence of this behavior had increased considerably. This level was maintained until the spawning, when there was another significant rise ($P < .01$) during the first post-spawning period.

No tail-slapping by the male was observed on the several days prior to the spawning, and during the three-hour pre-spawning interval, the frequency of tail-slaps remained low with relatively little fluctuation. Approximately this same frequency was observed during all the post-spawning observation periods.

Of the 25 pairs for which continuous records for the first hour were obtained, 100% of the females were recorded as tail-slapping at least once, but only 48% of the males. In the seven spawnings with two-hour continuous pre-spawning records, 71.4% of the males tail-slapped at least once.

HEAD-NODS. Following the transformation, head-nodding data for the female was characterized by a large number of zero frequencies and a small number of rather high frequencies. These did not fit Poisson distributions. At times, head-nodding was not clear cut and easy to recognize, and it is possible that a considerable amount of head-nodding passed unrecognized. Before the spawning, head-nodding activity was quite high (Text-fig. 4), at least for some of the



TEXT-FIG.5. Fluctuation in male and female nipping behavior before and after spawning.

females, and there was a still further rise after the egg laying.

The data for male behavior fit Poisson distributions quite closely. The low mean values indicate that this behavior occurred rather infrequently, and little fluctuation was noticeable before or after the spawning.

Of the 25 ovipositions from which continuous records were taken for the first pre-spawning hour, 84.0% of the females and only 20.0% of the males exhibited head-nodding at least once. Similarly, of the seven pairs where two-hour records were available, 100% of the females and 28.6% of the males head-nodded at least once. We may conclude that head-nodding is a typical female activity and that a small fraction of the males head-nod occasionally.

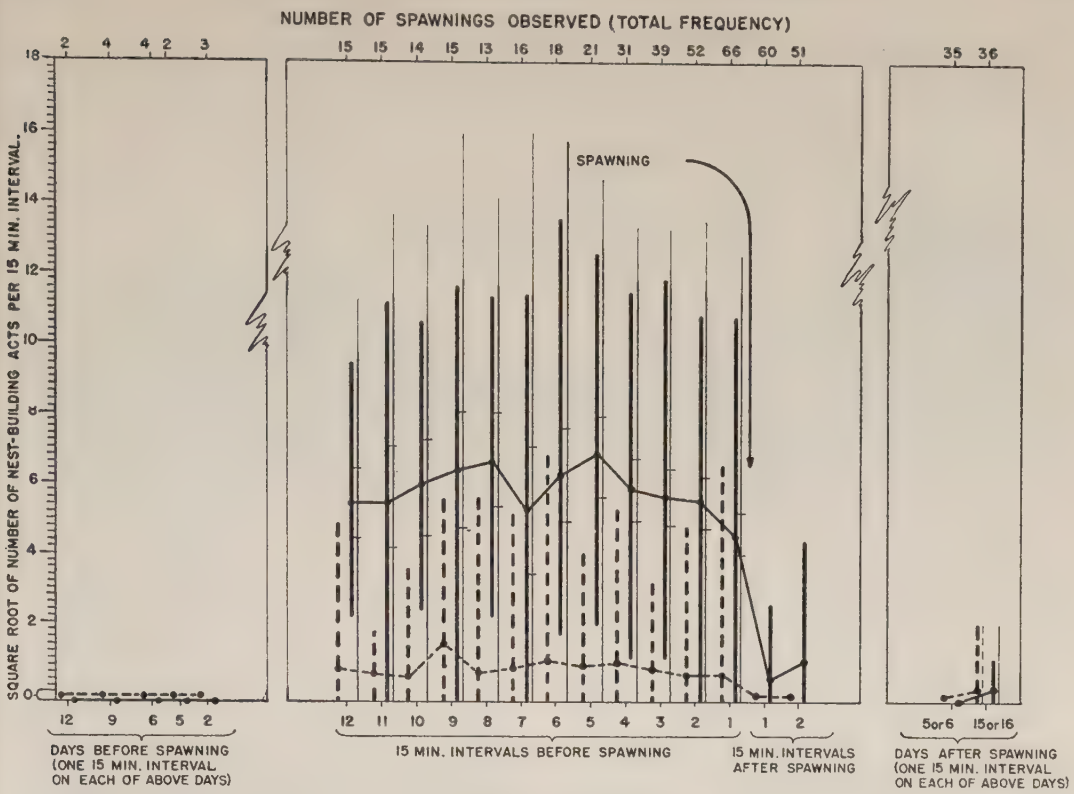
NIPS. Nipping data of both the male and female were treated as Poisson distributions. Both sexes displayed some nipping behavior on the several days they were observed before the spawning (Text-fig. 5). During the three-hour pre-spawning observation period, approximately the same amount of nipping was shown by both the males and females. After the egg laying there was a significant rise ($P < .01$) in the nipping frequency of the females. The rise in female nipping during the ninth pre-spawning interval may be significant ($P = .05$), but it was mostly due to a marked spurt of activity of a single female.

Analysis of the 25 spawnings where complete records for the first hour before spawning were taken showed that 68.0% of the females and only 28.0% of the males exhibited nipping behavior at least once. Where two-hour continuous records were available, 100% of the females, and 57.1% of the males engaged in some nipping activity. This suggests that practically all of the females and at least half of the males do some nipping before spawning.

NEST-BUILDING ACTS. On the several days before spawning, nest-building by either the male or female was not observed (Text-fig. 6), but by the third hour before oviposition, female nest-building activity had reached a rather high frequency. Since the presence of a nest and the occurrence of nest-building behavior was one of the more important criteria used to determine the imminence of spawning, and hence to ascertain the appropriateness of starting the observation, these data are likely to be somewhat biased in favor of early nest-builders. Actually at three hours before spawning, the average nest-building activity of the female may not be as high as that indicated by the data.

The drop indicated in the seventh pre-spawning interval appears not to be significant if the nest-building values of the fifth and seventh intervals are compared ($P = .13$). On the other hand, there is a noticeable downward slope between the fifth and first pre-spawning intervals, and when these two intervals are compared, the difference was found to be highly significant ($P < .01$). It is clear that female nest-building behavior drops off as the time for the laying of the eggs approaches, and it is gradually superseded first by nest-cleaning behavior (which is clearly distinguishable from nest-building), and secondly by nest-passing activity, which, as we shall see in the next section, is increasing as the nest-building frequency is declining.

Following the oviposition episode, nest-building activity dropped to a very low fig-



TEXT-FIG. 6. Fluctuation in male and female nest-building behavior before and after spawning.

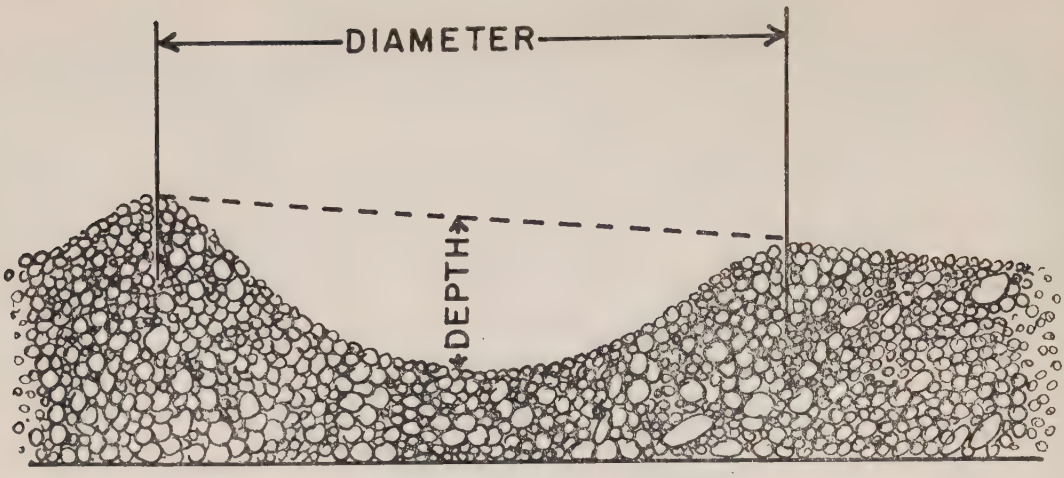
ure. On the 5th or 6th day nest-building by females was not observed, and on the 15th or 16th day only one nest-building act was observed during the 15-minute observation interval by one female out of thirty-six.

The data for the male was characterized by high frequencies of zero values and low frequencies of high values which nevertheless did not fit Poisson curves even after the aforementioned transformation. In contrast to the extensive nest-building activity of the female, that of the male was quite limited. Similar to the female, there is a downward slope in activity between the fourth and first pre-spawning intervals. However, the decline is not very pronounced and its statistical validity could not be readily ascertained. After the spawning the males no longer engaged in nest-building except for a single male which on the 15th post-spawning day nest-built four times during the observation interval. This male was paired with the one female, which was also observed to build a nest during the 15-day post-spawning interval. Two nests were present in the tank and it is apparent that this pair was approaching another spawning cycle.

Turning again to the 25 spawnings with continuous records for the first pre-spawning hour, it was found that 100% of the females and 72% of the males engaged in nest-building at least once. Of the seven pairs with continuous two-hour pre-spawning records, 71.4% of the males did some nest-building. It is probable that only a small percentage of males do not engage in any nest-building prior to the spawning.

Fifteen nests built by ten pairs were measured shortly after the spawnings. In each case the fish were first carefully removed without damaging the nests. Since in many cases the nests were oval, two diameters were taken, namely the short diameter, and at right angles to this the long diameter. The points used in these measurements are indicated in Text-fig. 7. The average short diameter was 11.8 cm., the average long diameter 13.2 cm., and the average depth 2.6 cm. The female fish (which as shown above are primarily responsible for the construction of the nests) varied from 10.7 gr. to 19.2 gr. with an average of 15.1 gr. The males were slightly heavier, weighing on the average 18.0 gr. There was no indication from these limited data of a correlation between size of fish and size of nest.

PASSING-NEST. The earliest nest-passing by the female was recorded for the eleventh pre-spawning interval, two and one-half hours before the egg laying (Text-fig. 8). Following the previously mentioned transformation, the data for this interval fit a Poisson distribution. The same is true for the records of the 6th, 8th, 9th and 10th intervals. The data for the 2nd to 5th and the 7th intervals consisted of a series of zero or very low frequencies and a smaller group of relatively high values, vaguely suggesting

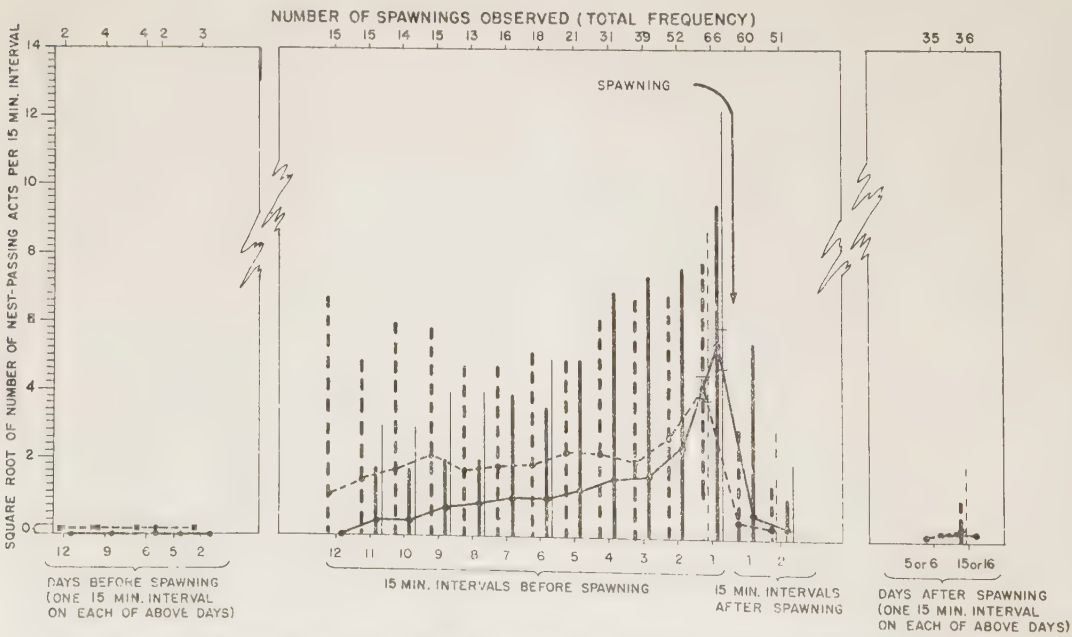


TEXT-FIG. 7. Diagrammatic section through typical *Tilapia* nest showing points used for nest measurements.

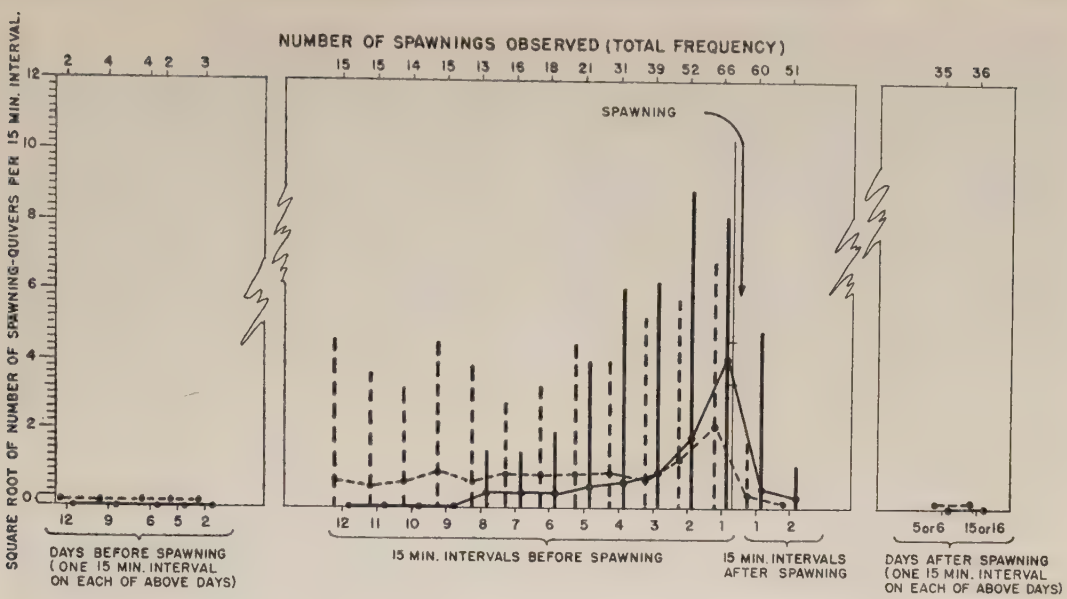
bimodal curves. The data for nest-passing for the first interval were normally distributed. These data indicate a gradually rising frequency of nest-passing as the spawning approached, with a sudden spurt of activity during the second and first intervals. After the egg laying, nest-passing activity of the female dropped to almost zero and none was recorded on the 5th or 6th and 15th or 16th days.

The nest-passing data of the male were normally distributed for the first interval. The records for the remaining pre-spawning intervals were highly skewed to the right with highest frequencies zero, which, however, did not fit Poisson series. While no nest-passing was recorded for the males on the several days prior to the spawning, a substantial amount of nest-passing was observed by three hours before the egg laying. This level of activity remained fairly constant until the second interval when it started to rise precipitously. However, during the first pre-spawning interval, the nest-passing activity of the female surpassed that of the male for the first time ($P<.01$). After the spawning, the frequency dropped to almost zero and nest-passing was not observed on the two post-spawning observation days.

Observations indicated that male and female nest-passing were not entirely independent of each other, and calculation of the



TEXT-FIG. 8. Fluctuation in male and female nest-passing behavior before and after spawning.



TEXT-FIG. 9. Fluctuation in male and female spawning-quiver behavior before and after spawning.

coefficient of correlation for the first pre-spawning interval yielded an r of + .63. This was transformed to Z = + .74 which is a highly significant correlation ($P<.01$). The nest-passing data for the remaining pre-spawning intervals appear to be comparably correlated, but the data do not readily lend themselves to this type of statistical treatment. Prior to the spawning, all of the males and females exhibited some nest-passing activity.

SPAWNING-QUIVERS. This behavior was not observed during the observation periods on the several days before the spawning (Text-fig. 9). Female spawning-quivers were first seen during the 8th pre-spawning interval, 1¾ to 2 hours before the egg laying. Their frequency gradually increased and reached a peak during the first pre-spawning interval. There was a marked drop to almost zero after the egg laying, and on the 5th or 6th days and 15th or 16th days none were seen.

A few male spawning-quivers were in evidence during the 12th pre-spawning interval, and a low level of this behavior was maintained until the second interval, 20 to 15 minutes before the egg laying, when there occurred an abrupt rise in frequency which terminated during the first interval. During the first post-spawning interval, a very few spawning-quivers were recorded, and none were seen thereafter. While a few of the males exhibited spawning-quivers long before the females, the peak of spawning-quiver activity of the females during the first pre-spawning interval was considerably higher than that of the males. However, the data did not permit further statistical analysis.

Selecting the 25 spawnings for which continuous records for the first hour before oviposition were available, it was observed that 96.0% of the females and 72.0% of the males showed at least one spawning-quiver during this hour. Similarly, in the seven spawnings for which two-hour continuous records were available, 100% of the females and 71.4% of the males were recorded as performing at least one spawning-quiver during these two hours. It thus appears that while all the females showed this behavior, in about a fourth of the males spawning-quivers could not readily be distinguished from nest-passing behavior. Since all of the females exhibited spawning-quivers and because of the sharp peak in the frequency of occurrence of this activity just before the spawning, this behavior can also be employed as an indicator of the approaching oviposition.

OVIPOSITION AND FERTILIZATION. The behavioral patterns considered thus far were recorded in terms of the number of times that the acts occurred during a short interval of time (i.e., 15 minutes), and the relative infrequency of some of this behavior accounts in part for the marked skewness of the distribution curves. On the other hand, the oviposition data which follow, and the data concerning the reactions of the male and female to the eggs and young, are based upon the total frequency of the behavior during a given spawning, and as might be anticipated, these data approximated more closely binomial distributions which could be treated as normal curves.

A nest-passing act by the female during which eggs were oviposited was counted as a single oviposition movement. A nest-passing act by the male when eggs were present in the nest was recorded as a fertilization movement. Actual contact with the eggs was not considered essential as a criterion for a fertilization movement, although in most

instances the male rubbed his genital tube over some of the freshly laid eggs.

In 76 observed spawnings, the mean number of oviposition movements by the female was 3.41 ± .13 with a standard deviation of 1.1 movements. The mean number of male fertilization movements was 3.46 ± .15 with a standard deviation of 1.3. The difference between the means is .05 ± .2 which indicates clearly that the number of oviposition movements of the female does not differ significantly from the number of fertilization movements of the male. Finally, there is a significant positive correlation ($r = +.48$, $z = +.52$, P calculated from $\frac{z}{\sigma z} < .01$) between these two activities, indicating that the number of times the males fertilize the eggs is partly related to, and probably dependent upon the number of oviposition acts of the female.

PARENTAL BEHAVIOR. In a total of 76 observed spawnings, the male alone picked up the eggs in 62 cases (81.8%), the female picked up the eggs in 6 cases (7.9%) while both male and female participated in this activity in 8 cases (10.5%).

The time after the beginning of oviposition for the male to start picking up eggs varied from 20″ to 2′10″ with a mean of 1′3″ ± 3″ and a standard deviation of 23″. For the female this interval varied from 3′18″ to 11′14″ with a mean of 7′59″ ± 1′22″ and a standard deviation of 3′17″. The difference between the means of these two distributions is obviously significant, and from these data we may conclude that the male starts to pick up the eggs as soon as the oviposition has terminated, while the female allows several minutes to elapse before she will collect any of the eggs still available. Here then is an apportioning mechanism which results in the observed fact that the male usually incubates the eggs, and the female does so on infrequent occasions.

Eggs remain in the nest available to the female under two circumstances. First, if the male's mouth is of insufficient size to contain all of the eggs, a few may be left over in the nest. This was the situation in case 1 (Table I) where a small male was paired with a large female. It was quite clear to the observer that in this instance not all of the eggs could fit into the male's mouth. Secondly, eggs would be available to the female when the male behaved atypically and did not touch the eggs. In three of these cases males had released broods seven to twelve days previous to the spawnings, and this may be a contributing factor causing the lack of response of the males to the eggs.[14] In most instances where the eggs remained in the nest for any length of time, the females would chase, nip and court the males. In a few cases, the latter retaliated and violent fighting ensued; as a result the nests were destroyed and the eggs scattered. In cases 3, 6, and 7 (Table I), as soon as the female began to pick up the eggs, the males followed suit and both gathered up the eggs simultaneously. The typical pattern when eggs are left in the nest may be summarized as follows:

(1) Immediately after the eggs are oviposited and inseminated, there is often a period of extreme quiescence lasting a minute or two.

(2) This is followed by a period in which the female appears to be inhibited from approaching or touching the eggs, but at the same time she seems to be excited by the eggs, resulting in active nipping, chasing and courting of the male who sometimes responds similarly.

(3) After several minutes the inhibitory action of the eggs begins to diminish; the female now approaches the nest, pokes around the eggs, and eventually picks them up. It was at this time that several of the recalcitrant males listed in Table I also approached the nest and in a few cases started to pick up eggs ahead of the female.

It is suggested that in cases 2 to 8 (Table I), chasing, nipping and courting by the female, and also her poking around the nest, sufficiently stimulated the male to pick up the eggs, thereby completing the pattern.

Once started, the length of time it took for males to gather up the spawn varied from 2″ to 1′45″ with a mean of 13″ ± 2″ and a standard deviation of 16″. The high variability noted here is a result of two exceptional cases, one where the male took 1′7″ and in the other 1′45″. In the remaining 60 spawnings, the time was less than 46″. On the other hand, six females took from 35″ to 3′ with a mean of 2′6″ ± 22″ and a standard deviation of 51.7″. Thus we see that not only does the female wait longer before starting to pick up the eggs, but once started she performs this task at a significantly

TABLE I.

Time from the Beginning of Oviposition for Eggs to Be Picked Up. Eight Cases Where Both Male and Female Engaged in This Activity.

	Male		Female	
Case No.	Start	Finish	Start	Finish
1	25″—	50″	7′15″—	
2	11′00″—	11′30″	6′50″—	10′10″
3	3′00″—	4′00″	2′30″—	4′00″
4	4′05″—	4′30″	4′15″—	4′30″
5	2′05″—	5′00″	4′30″—	5′00″
6	4′10″—	5′10″	4′10″—	4′55″
7	6′24″—	10′30″	5′50″—	6′36″
8	3′50″—	4′00″	1′25″—	3′30″

[14] On the other hand, recent observations by Aronson and Holz-Tucker (unpublished) reveal that males in the process of incubating young may on occasion fertilize and pick up a new batch of eggs.

slower rate. In most cases, the males gathered up the eggs rapidly and then kept poking around the nest for some time. Thus any scattered eggs were quickly recovered. Some of the females, on the other hand, would pick up part of the eggs, swim away from the nest, return and pick up more eggs, swim away again, and so forth.

The egg-gathering records for the female were necessarily limited by the behavior of the males as noted above. It was therefore considered appropriate to use for comparison data from other experiments. Aronson and Holz-Tucker (unpublished data) observed the spawning of an isolated female that could see another female in an adjacent tank. The ovipositing female took 24′ to start gathering up the eggs and the process itself took 1′25″ to complete. Similarly, we observed the spawning of a completely isolated female. This female did not start to pick up the eggs for 13′5″. She took 1′15″ to gather up most of the spawn, but left six eggs which she did not pick up for another eight minutes. A large number of normal females were paired with males suffering various types of brain lesions (Aronson, in manuscript). In 27 spawnings, these females took on the average 12′2″ to start picking up eggs and an average of 1′15″ to complete the job. Hence these data support our original conclusions. However, it is likely that in our first observations, the mean time for the six females to start picking up the eggs is somewhat low, while the time it took to complete the process may be a little too high. It is of interest to note that in a few spawnings the females seemed unable to carry all of the eggs that they themselves had laid.

Both the male and female are capable of successfully incubating the eggs. The percentage of spawnings in which young were recovered at the termination of the incubatory period is shown in Table II. Where the spawnings were not witnessed, the slightly higher score made by the males may be accounted for by a possible failure to record a few cases where the spawn was swallowed immediately after the oviposition, and before it was observed. The data for the third set of observations are taken from a second experiment, (Aronson, 1945). These spawnings were also not witnessed. In this experiment, aquarium conditions were considerably improved by the use of aquarium filters, thus avoiding any changes of water. The young were forcibly ejected from the parental mouth on or about the tenth day after spawning and were counted immediately, thus largely eliminating the possibility of losses through cannibalism.

Even with these improved techniques, only 40% of the males released viable fry. Two factors account for this low yield of young by the males. First is the failure of the eggs to be properly fertilized, or death of the embryos, with subsequent disintegration of the eggs. A second factor is swallowing the spawn. The relative importance of these two factors will now be considered.

If freshly laid unfertilized eggs are placed in a jar of *Tilapia*-conditioned water which is kept at approximately 26° C., very few of the eggs will show any gross signs of degeneration before 24 hours. Starting with the second day, however, some of the eggs will have decomposed, and in all cases few if any intact eggs remain after the tenth day. As to the variation in the length of the incubation period, it will be seen in columns 6 and 7 of Table III that females may carry unfertilized eggs for as long as ten days, after which time it may be assumed that all have decomposed. Note particularly that in almost 80%[15] of these cases, the dead eggs were retained longer than one day, and it is highly probable that in many of these cases the eggs were carried until they were quite degenerate. It was not unusual to examine the contents of a male's or female's mouth and

[15] Since the presence of incubating eggs was checked only twice daily, spawn swallowed shortly after oviposition might have been overlooked. Hence this figure may be a little too high.

TABLE II.

Per Cent. of Spawnings in which Young Were Recovered.

	No. of spawnings in which males incubated eggs.	No. of males releasing young.	% of males releasing young.	No. of spawnings in which female incubated eggs.	No. of females releasing young.	% of females releasing young.
Spawnings witnessed.	68	22	32.4	14	3	21.4
Spawnings not witnessed.	85	33	38.8	2	0	0.0
Spawnings not witnessed, 2nd experiment.	70	28	40.0	4	4	100.0

TABLE III.

Variation in Length of Incubatory Period.

Length of incubation.	NO YOUNG RECOVERED						YOUNG RECOVERED			
	Incubated by males[1].		Incubated by females[1].		Incubated by females[2] (unfertilized eggs).		Incubated by males[3].		Incubated by females[1,4].	
	No. of males.	Per cent. of males.	No. of females.	Per cent. of females	No. of females	Per cent. of females	No. of males.	Per cent. of males.	No. of females.	Per cent. of females.
0- 1 hr.	1	2.2	5	45.5						
1- 8 hr.	1	2.2	1	9.1	54	20.1				
8-24 hr.	6	13.3	0	0.0						
2 days.	7	15.6	1	9.1	54	20.1				
3 "	13	28.9	1	9.1	34	12.7				
4 "	10	22.2	2	18.2	44	16.4				
5 "	1	2.2	0	0.0	31	11.6				
6 "	2	4.4	1	9.1	19	7.1				
7 "	1	2.2			19	7.1	1	1.2		
8 "	0	0.0			6	2.2	1	1.2		
9 "	0	0.0			5	1.9	1	1.2		
10 "	2	4.4			2	.7	2	2.5		
11 "	1	2.2					12	14.1		
12 "							8	9.4		
13 "							18	21.2		
14 "							12	14.1		
15 "							9	10.6		
16 "							4	4.7	1	33.3
17 "							11	12.9	1	33.3
18 "							2	2.5		
19 "							1	1.2	1	33.3
20 "							3	3.5		

[1] All spawnings witnessed.

[2] Females isolated from males. Spawnings not witnessed. Incubation intervals less than 1 day were recorded as one day, but some short intervals might have been missed. Data from Aronson (1945).

[3] Some spawnings not witnessed. Includes data from Aronson (1945).

[4] The young from the four females of the 2nd experiment indicated in Table II were forcibly removed from the parents' mouths on the 12th day. Hence these cases could not be included in this table.

find that the fish had been carrying a mass of badly decomposed eggs, or a mixture of decaying eggs and viable embryos. From the appearance of the eggs it was frequently apparent that the fish had been carrying the dead eggs for many days. In columns 2 and 3 are listed the durations of the incubatory intervals for males carrying fertilized eggs. It will be noted that in 17.7% of the cases, the spawn was swallowed within 24 hours. The indirect evidence cited above leads to to the conclusion that these eggs were swallowed because of some failure of the male's incubatory mechanism, whereby the male failed to discriminate between eggs and food. On the other hand, those egg masses which were retained in the mouth for a number of days were only swallowed when they had become extensively decomposed. It should be noted in passing that decomposed eggs are never found in the tanks, and it is assumed that they are swallowed rather than spat out. The stomach contents of several males were examined shortly after the egg layings, while the males were carrying eggs. In two of these cases a few eggs were also found in the stomachs.

Columns 4 and 5 show that in 54.6% of the spawnings in which eggs are picked up by the females, they were swallowed within 24 hours and in most cases within the first hour after spawning. Although these data are limited, they indicate that the female's incubatory mechanism is not as dependable as the male's, and that the female fails to distinguish eggs from food much more frequently than does the male.

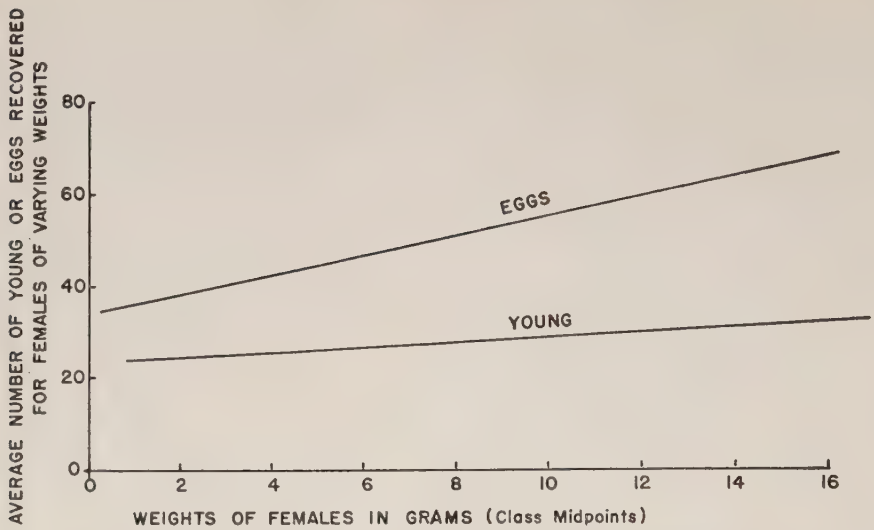
The length of incubation by the male in cases where young are recovered is shown in columns 8 and 9 of Table III. These data fit closely a normal curve, and from them we have determined a mean incubatory time of 13.8 ± .27 days with a standard deviation of ± 2.6 days. This would give us a theoretical range of 6 days to 22 days. The few cases in which the female successfully reared young fall well within this range.

Thus far, only the presence or absence of eggs and developing embryos have been considered. Now, the relative sizes of the spawn and brood will be examined. A new group of pairs was established, and on the day of or day after oviposition, the spawn was ejected from the male's mouth and was counted. This count may be taken to represent fairly accurately the number of eggs laid by the female, since, in most instances, all of the eggs are picked up and few if any are swallowed. Eighty females whose mean weight was 7.15 ± .38 gr. deposited an average of 49.7 ± 1.96 eggs.

In a second group of 31 pairs in which the average weight of the females was only slightly less (5.6 ± .38 gr.), the males were allowed to incubate the eggs and the fry were counted soon after their release. Here it was found that the average brood size was only 23.9 ± 2.9 young. It was thought at first that this smaller brood size might be attributed to the lesser weights of our second group. To examine this hypothesis the body weights of the females that had just oviposited were compared with number of eggs in the spawn. A low order positive correlation was found, which was probably significant ($r = +.23$ or $z = +.236$; P calculated from $\frac{z}{\sigma z} = .05$). A similar comparison of the weights of females (determined immediately after oviposition) with the size of the brood that was eventually recovered after being incubated by the male partner did not yield a significant correlation ($r = +.10$ or $Z = +.10$; P calculated from $\frac{z}{\sigma z} = .6$). When two regression lines are plotted (calculated by the method of least squares), one for the rise in number of eggs oviposited as body weight increases, and a second for the change in number of young recovered as body weight increases (Text-fig. 10), the relationship involved becomes clearer. From these regression lines in Text-fig. 10, it can readily be seen that for females of the same body weight, the number of young successfully incubated is considerably smaller than the number of eggs laid. This loss can best be accounted for by the failure of some of the eggs to be fertilized and by the death of some of the embryos. Since brooding fish have never been observed to spit out decomposed eggs or embryos, and since such material has rarely been observed on the gravel substrata of the aquaria, it is assumed that the incubating fish somehow manages to sort out and swallow this dead matter.

These data also indicate that while larger females tend to lay a greater quantity of eggs than smaller females, the number of fry successfully brooded by the males remains constant regardless of the weights of the females and hence of the magnitude of the spawn. Therefore the mortality of eggs and embryos must be directly proportional to the size of the female and hence to the number of eggs laid. Since the larger females were in most cases older, this difference might be based upon an aging factor. It is also conceivable that such increased mortality was due to overcrowding in the male's mouth during incubation.

It is an interesting fact that incubating *Tilapia* generally carry some gravel intermingled with eggs. Of 63 fish examined on the day or day after the egg laying, 95.2% were carrying one or more pieces of gravel. Generally between 25 and 50 pieces (commercial grade No. 2) were found along with the eggs, and occasionally the count went well over 100. The possible significance of this fact is not known at present. It is not clear whether or not the gravel is picked up accidently along with the eggs, and whether this behavior bears some relation to the survival of the embryos. For example, it is possible that since the eggs and gravel are continuously churned around in the mouth, the



TEXT-FIG. 10 Regression lines showing relation of body weights of females to number of eggs laid during each spawning and relation of body weights of females that spawned, to number of young recovered immediately after their release by the incubating males.

latter might serve to rub off fungi or ectoparasites from the developing fish.

It is important to note that there is considerable variability in the number of days that given parents may incubate their young. It is therefore to be expected that at the time of release, the broods carried longest will be the ones furthest advanced in development. This, generally speaking, is found to be true. Thus, fry released in less than ten days still have a large yolk sac and their swimming activity is sporadic, whereas young incubated for longer intervals show little or no trace of the yolk sac, also their swimming ability is developed to the stage where they are well able to elude their enemies if reasonable shelter is provided. A complicating factor is that, as can be seen from the few samples in Table IV, there is a considerable difference in the rate at which the fry grow within the parental mouths. Thus the average size of a given brood incubated for 22 days was barely larger than another one incubated only 15 days. Similarly, a given brood retained in the mouth for only 11 days reached the same average size as another brood incubated for 16 days. It is possible the number of young in the brood may somehow be related to growth rate; however, our limited data on this point in Table IV do not suggest such a relationship. It is also of interest to note that the variation within the brood was quite low, the average coefficient of variation (V) for nine broods being 3.7. This state of affairs is in striking contrast to the great variability ($V = 15 \pm 1.60$) which resulted when a brood was kept together in a stock tank from the time of release to maturity (Aronson and Holz-Tucker, in manuscript).

DISCUSSION.

In most vertebrates the characteristic mating behavior patterns of the two sexes are distinctly different. Thus in the rat, the reproductive habits of which have been analyzed most intensively, the typical pattern of the estrous female, lordosis, is only occasionally exhibited by the male (Beach, 1938, 1945). Similarly, the typical male pattern of ear-wriggling, mounting and pelvic thrusts is seldom seen in the female (Long and Evans, 1922; Hemmingsen, 1933; Beach, 1938).

The sex difference in behavior generally is very clear although relative rather than absolute. Under special conditions males may be induced to exhibit female-like behavior, and the reverse can also be accomplished (Beach, 1941). The conditions producing such results often are very special in nature. Thus for example, the well known fact that estrous cows frequently exhibit male-like mounting behavior may very well result from the almost universal custom of segregating the cows from the bulls. Similarly Beach and Rasquin (1942) explain in part the high incidence of masculine behavior in their female rats as the result of repeatedly testing two females together. These authors are also aware of the possibility that the females of their particular colony may have been more active in a masculine direction than are females from most other stocks. However, we are concerned with the fact that disparity of behavior between sexes is general among the vertebrates.

A survey of the literature indicates that in reptiles a behavioral dichotomy of the sexes appears to be the rule, and the writer's extensive investigations of the sexual be-

TABLE IV.

Relation Between Average Size[1] of Young in Brood and the Number of Days the Brood Was Incubated.

No. of days young were carried.	No. of fry in brood.	Average length of fry[1] (mm.).	Coefficient of variation.
10	13	9.2 ± .08	2.9 ± .57[2]
11	19	10.6 ± .10	4.0 ± .65
11	3	10.4	.....
11	8	9.8 ± .09	2.8 ± .70
12	44	10.8 ± .06	3.9 ± .41
14	18	9.4 ± .11	5.1 ± .85
15	82	11.2 ± .04	3.3 ± .26
16	58	10.6 ± .06	4.4 ± .40
16	38	10.6 ± .06	3.7 ± .43
22	58	11.5 ± .05	3.4 ± .31

[1] Length from tip of mouth to end of tail fin.
[2] Standard error of the coefficient of variation.

havior of the tailless amphibia have shown that in the Anura, male and female sexual behavior are quite specific with only occasional evidence of bisexual behavior (Noble and Aronson, 1942; Aronson, 1943, 1943a, 1944).

In many birds these distinctions are less clear. Thus in the pigeon, billing and bowing are common to both sexes (Whitman, 1919), and while it is usual for the female to squat and for the male to mount, copulation not infrequently occurs with the positions reversed (Carpenter, 1933).

While all vertebrates appear to possess the neuromuscular and hormonal mechanisms capable of eliciting most elements of the mating pattern of the opposite sex (Beach, 1942, 1947), morphological differences, particularly in the genitalia, hormones and other genetic factors, greatly limit the incidence, completeness and effectiveness of such behavior. Thus in the majority of vertebrates, behavior patterns characteristic of the male or female are readily distinguished.

In contrast to this typical vertebrate condition, *Tilapia* appears to represent an extreme condition. None of the patterns of reproductive behavior investigated are entirely characteristic of either sex. Qualitatively, male and female courtship and spawning behavior are exactly alike. Even in the acts of oviposition and fertilization, the overt motor patterns are the same in both sexes. Both fish swim slowly over the nest and rub their genital tubes on the substratum. The one observable difference occurs when eggs extrude through the genital aperture of the female, while the male's genital tube releases sperm, which, however, are invisible to the naked eye. It is only when the frequencies of the various reproductive acts are considered that behavioral differences between the sexes become apparent. It is true even so that in *Tilapia* sex differences in behavior depend in some cases on the time interval before the spawning. Thus, as we have found, the females exhibit much more courtship and do most of the nest-building. Males do more nest-passing than the females at one to two hours before the spawning, but at 15 minutes prior to oviposition we find this relationship clearly reversed. After the spawning, both qualitative similarity and quantitative dichotomy are still in evidence. Thus males wait on the average only 1.3′ before they start to pick up eggs; whereas females require on an average 7′59″. Also, males pick up the eggs much faster than the females, and are less prone to swallow their eggs.

In some of the patterns, as for example head-nodding, the quantitative difference between male and female frequency of the act is sufficiently large that such behavior could possibly be called a female pattern. However, our data have shown that in 25 pairs where continuous records for the first hour were available, almost one-third of the males exhibited some head-nodding. It is highly probable that if the entire span of the pre-spawning sex behavior could be observed, an even greater percentage of the males would be found to perform a minimal amount of this behavior. Bisexual or homosexual activity has generally been thought of as a recognizable intrusion of the characteristics of behavior in one sex to a greater or lesser extent into the behavior patterns characteristic of the opposite sex. Such partial observations of sex dichotomy are known to occur in a limited portion of the population or under special circumstances such as segregation. Thus we are justified in considering bisexual or homosexual behavior a rather restricted phenomonon in most vertebrates. It follows that in the case of *Tilapia* none of the patterns should be relegated to one particular sex as is generally done in the higher vertebrates.

One might hypothesize that this situation in *Tilapia* represents a primitive condition in the evolution of reproductive behavior patterns. This, however, is doubtful since cichlids are a highly specialized family of

teleosts, and on the other hand clearly recognizable, sexually divergent mating patterns are in evidence in some of the anatomically more primitive fishes. While our study of the described condition concerns *Tilapia*, it is apparent from the literature that qualitative similarities and quantitative differences such as we find between male and female sexual behavior in this species will be found to a greater or lesser extent in all cichlid fishes, and may well be true of several other families of fish.

Rather than being a primitive condition, we might view these behavior patterns of *Tilapia* as adjustments (in an evolutionary sense) to a specialized mode of reproduction in which the similarity of the sex behavior patterns has a considerable adaptive value. For the post-spawning parental behavior this point is fairly evident. If both sexes are capable of rearing the young, there is less likelihood of lost or wasted spawn. If we look upon the action of courtship as a mutually stimulating and a synchronizing mechanism as well as one which keeps the pair together, one might expect the sexes to develop comparable mechanisms to accomplish the same outcome when not limited by morphological dissimilarities.

Not all behavioral disparities between the sexes in *Tilapia* are readily understandable. On several occasions, males exhibited considerably more courtship activity than the females of given pairs. In no case did such excess lead to a spawning. One observation showed a male in a stock tank courting at a very high frequency as he swam around the enclosure. In the same aquarium a female was engaged in building a nest. Actually she did not court in relation to this sexually active male, but rather her activities had to do with two other males in the territory. The significance of excessive courtship by males is not clear. It is possible that it represents the equivalent of bisexual behavior, that is, of males behaving like females.

In this study we have found it convenient to group certain activities such as the throat-puff, body-quiver, tail-slap and head-nod under the category of courtship, as distinct from subsequent items of the reproductive series, namely nest-building, nest-passing, spawning-quivers, oviposition and fertilization. However, no sharp line of demarcation is implied between these. If we follow the functional definition of courtship as previously stated (page 136), one cannot altogether exclude the latter group of patterns from the courtship category. However, a separation on the basis of functional or adaptive significance seems to be in order. Thus courtship behavior is mainly concerned with the formation and maintenance of the pairs while the latter activities have most to do with the immediate preparation for spawning, as for example the building of the nest and the physiological preparation for oviposition and fertilization. Also there are indications of an organic separation. It is of interest to note in this connection that in our observations on the several days before spawning, most of what we are terming courtship activities were seen at one time or another, but the acts of nest-building, passing-nest and spawning-quivers were never recorded. Thus in general reproductive behavior tends to arise and function in group fashion.

The quantitative records show that all of the courtship responses of the female increased in frequency directly after spawning. The same was true for nipping. Two factors appear to be responsible for this increased activity. The first is a physiological change consequent to oviposition, and the second is the presence of eggs. While we have not attempted to analyze the relative influence of these two factors, several observations are of interest here. First, the observed heightened courtship activity generally lasts several hours and subsides gradually. Secondly, the activity continues long after the eggs have been removed to the male's mouth. The freshly laid eggs might possibly release some type of chemical stimulus, but the evidence for this is not forthcoming. Moreover, if newly oviposited eggs are presented to males and females that have not spawned recently, such eggs are generally eaten within a short time, and they do not stimulate either courtship or nipping. The effect of this heightened activity is not apparent in most of the spawnings, but in the few cases where the males are slow in picking up the eggs, the courting seems to attract the male to the nest and stimulates him to gather up the spawn.

It has long been recognized that certain external morphological characteristics of an animal, together with specific modes of behavior, may act as exciting stimuli to other members of the species (and sometimes to members of another species) for the mediation of specific behavioral responses. Lorenz (1935, 1937) has developed this concept as a cornerstone of his theory of instinctive behavior. The stimulus or group of related stimuli bringing forth a reaction are called "releasers," the responding individual is designated as the "companion." Mutual instinctive responses of companions are sharply separated from learning processes although some modifications of the former are recognized. Furthermore, according to this view the release of every unconditioned reaction is considered to be dependent on a special central nervous mechanism which is called the "innate releasing schema" (Lorenz, 1935) or "innate releasing mechanism" (Tinbergen, 1939, 1948).

These hypotheses have become quite popular on the Continent. In this country they have received some consideration by students of bird behavior, but they are largely out of tune with the findings and interpretations of a large segment of the American experimental psychologists (Lashley, 1938) who in general have paid little attention to the

Lorenz movement. To say that a special "innate releasing mechanism" exists for every unconditioned reaction implies an extreme localization of function within the brain, a claim that is without special support in this country. Here the more popular view is that most responses are capable of being elicited by a broad array of well separated stimuli (Beach, 1942, 1947) and are not exclusively dependent upon any single stimulus or group of stimuli. Moreover, there is here a growing tendency to think of innate and learned factors as closely interlocked in their influence on behavior (Schneirla, 1941, 1946) with the view that in the higher vertebrates at least, purely innate behavior patterns as entities may be simply matters of a convenient terminology doubtfully related to reality. Lack (1940) has criticized Lorenz's view as being too simple. He points out that in many cases the designated releasers may not be the sole characters that bring forth the response. Rand (1941) has been to date Lorenz's severest critic. According to Rand, the releasing characters are by far too limited, and the releasers and responses are mostly unidentified. The reality of releasers has accordingly not been demonstrated but remains presumptive. Actually the experimental analytical approach to behavior is not only untried by Lorenz, but its validity is denied. Finally, according to Rand, there is in Lorenz's treatment a negativistic approach which denies the possibility of ever being able to elucidate the fundamentals of behavior.

Tinbergen (1939) has modified Lorenz's hypotheses in several respects. First, releasers are called "signals" or later "sign stimuli" and are subdivided into releasing stimuli and directing stimuli. More important, Tinbergen recognizes a closer relation than does Lorenz between innate responses released and modifiable factors such as learning, endocrine reactions and neural processes (summation, conditioning and "higher mental processes"). Most important is Tinbergen's recognition of the validity of the experimental approach, and his attempts, mostly by means of artifacts and models, to demonstrate releasers in this manner. Even so, it must be emphasized that Tinbergen sees releasers as very specific and limited morphological and behavioral characters which during the unfolding of a complex pattern of response will hold to a relatively rigid sequence.

Seitz, a follower of Lorenz and Tinbergen, has analyzed the behavior of two related cichlid fishes, namely a small Egyptian mouthbreeder, *Astatotilapia strigigena* (1940) and the jewel fish, *Hemichromis bimaculatus* (1942) in terms of the releaser concept. Seitz recognizes whole series of very specific releasers which call forth specific responses and which lead in an orderly manner to the spawning. These he has summarized in schematic form (1940, p. 82; 1942, p. 100). Thus, in *Astatotilapia,* the presence of a female releases a change to mating coloration in the male, and this change in its turn releases a slight but not significant color change in the female. The presence of the female also releases a mode of behavior called by Seitz an introductory presentation which in turn brings forth a passive response in the female. This in turn releases a complex of movement and color change called by Seitz a "Fegebalz" (lit., sweeping courtship dance). This Fegebalz of the male releases a following reaction on the part of the female, which in its turn releases circular swimming in the male around the spawning site. The circular swimming then releases a strong following reaction of the female to the spawning site which in turn brings forth a response whereby the male slips under the female. This releases circling movements in the female which in turn release the same movements in the male. The circling movements of the male call forth additional circling movements by the female. These release the oviposition movements and the latter release the fertilization movements of the male.

Our experiments were not designed to test the releaser concept and this discussion is not intended as a critique thereof. However, we were interested in learning to what extent our data would or would not support the releaser hypothesis or fit into that pattern of thought.

The significant correlation between male and female nest-passing behavior appeared most likely to fit in with this concept if we were to assume that nest-passing of male and female released a like behavior in the opposite sex. However, we had on record any number of cases where the females were very quiescent, exhibiting little or no courtship or pre-spawning behavior of any kind, and yet the males nest-passed consistently. Of course, the nest itself might be a releaser of nest-passing, but this would contradict a large portion of our data where nest-building by the female and the presence of a well-formed nest was not followed by nest-passing on the part of the male. Similarly in the spawning of the completely isolated female previously referred to, the order of magnitude of nest-passing behavior was well within the range of variability of our control pairs. Yet there was nothing in that situation which could be considered a releaser. In an attempt to follow the lead of Seitz, we could possibly view the various courtship patterns previously described as releasers. For example, the approach-throat-puff of the female might be construed as a releaser of similar behavior by the male which in turn might be thought of as releasing female nest-building behavior. This may be especially so since an approach-throat-puff by a female was often followed by a similar pattern in the male, and soon thereafter the female turned to the construction of the nest. However, no consistent pattern of this type was in evidence. Female throat-puffs were also followed by almost any of the other courtship patterns or by no particular re-

sponses of the male. Again, female nest-building was sometimes preceded by the throat-puffs but often by head-nods, tail-slaps or body-quivers. It is recognized that in general observation, that is in "just watching" these fish, one could easily gain the impression that certain acts are in effect releasers, and others a response to these releasers. However, when observational technique involves an orderly and complete quantification of response according to condition of occurrence, the data do not support such an interpretation.

We are inclined to view the courtship and pre-spawning items of behavior together with the territory and nest as having a general stimulatory effect upon the other member of the pair which would tend to raise the level of sexual excitability in the latter. Or, to put the matter in another way, the given conditions may serve to lower the threshold for the elicitation of various courtship and pre-spawning patterns. Here the particular response obtained would depend upon a whole complex of factors including the neural threshold, the immediate topographic relation to the partner, the territory, the nest and other environmental conditions, as well as the internal physiological balance of the individual at the moment. In this sort of system, no specific releasing stimuli may be properly postulated. For example, a series of weak or only partially effective tail-slaps by the female might bring forth a response in the male similar to one very effective approach-throat-puff. Moreover, as the general level of excitability of both members of the pair increased, there would be a gradual shift in the statistical probability of the elicitation of a given type of response. In other words, throat-puffing during the early stages of the pre-spawning history of a pair might bring forth additional throat-puffing or other phases of the courtship, while later, such behavior might elicit return to the nest or nest-passing. As spawning approached, nest-passing behavior of one member of the pair was often followed by like behavior of the other member of the pair, but this was often interrupted by some of the early phases of courtship such as head-nodding and tail-slapping. In many of the records, interruptions of the smooth flow of passing-nest and spawning-quivers were noted within minutes of the actual oviposition. While these data do not altogether contradict the releaser concept, it is believed that these findings can be more satisfactorily understood by adhering to a considerably more generalized interpretation of the complexity and effectiveness of the stimuli than the "releaser concept" implies.

Seitz (1940) and Tinbergen (1948) in their discussion of releasers refer to the "rule of heterogeneous summation" which states that the release of a given behavior pattern may result from the summation of several different stimuli. Tinbergen also emphasizes that "high internal motivation may cause the reactor to respond to all objects offering the minimum adequate external stimulation." Finally, Tinbergen observes that some releasers have a general excitatory influence, rather than to direct the reactor's response. If these three principles noted here are sufficiently expanded, some of the major objections to the releaser concept are thus overcome, and except for the sharp lines drawn between instinct and learning processes, we begin to arrive at a common ground for the understanding of the nature of sexual behavior.

Summary and Conclusion.

Qualitative descriptions and quantitative measurements of the patterns of reproductive behavior of the African mouthbreeding cichlid fish, *Tilapia macrocephala* (Bleeker), have been presented. These patterns have been grouped into three categories. The first, namely courtship, includes head-nods, approach-throat-puffs, body-quivers and tail-slaps. Most of the females exhibited these courtship items during the observation periods, and at a relatively high frequency. The males performed these courtship acts at a considerably lower frequency. A high percentage of males showed some tail-slaps and body-quivers, and it is believed that if the entire spans of the pre-spawning activity of the pairs could have been observed, all of the males would have performed these courtship patterns. On the other hand, it appears that a measurable portion of males do not head-nod or approach-throat-puff prior to the spawning.

It is hypothesized that courtship behavior is an expression of the level of excitability of the individual. It may be thought of as a trophallactic process which through mutual stimulation serves to regulate the behavioral activities and physiological processes of the male and female so that well synchronized spawnings result.

Nipping, which is closely related to courtship and which also appears to be mutually stimulating, was performed equally by the male and female before the spawning, but nipping on the part of the female rises sharply directly after oviposition. Similar post-spawning increases on the part of the female were noted for all of the courtship patterns. It is suggested that the physiological changes following oviposition plus the presence of eggs are the factors responsible for this heightened activity. During the inter-spawning interval, a low level of courtship is in evidence, especially on the part of the females.

The second group of reproductive patterns includes those acts which are concerned with the immediate preparation for spawning. Included here are nest-building, nest-passing, spawning-quivers, oviposition movements and the act of fertilization. Considerably more nest-building is exhibited by the

female than by the male, but it is likely that all males do some nest-building before every spawning. With passing-nest and spawning-quivers the frequency is somewhat higher for the males an hour or so before spawning, but at 15 minutes before spawning this relationship is clearly reversed, with the females at the height of their nest-passing and spawning-quivers. A significant correlation between male and female nest-passing during the first pre-spawning interval suggests that this behavior is mutually stimulating. The mean number of oviposition movements of the female did not differ significantly from the mean number of fertilization acts of the male. Moreover these behavior patterns are highly correlated, suggesting that the number of times the male fertilizes the eggs is partly related to and probably dependent upon the number of oviposition movements of the female. In contrast with the courtship patterns, behavioral items in the present category were not observed during the inter-spawning interval.

The third category of reproductive acts are those associated with the care of eggs and young. Males start picking up eggs on an average of 1′3″ from the beginning of oviposition. Females, if given the opportunity, took on the average 7′59″. This is the apportioning mechanism whereby males usually incubate the eggs, and females do so only on infrequent or special occasions. Similar quantitative differences were found in other phases of the parental pattern. Thus females gather up the spawn more slowly and are more prone to swallow the eggs.

A low order positive correlation was found between the size of the female and the number of eggs laid during a given spawning. Since brood size shows no correlation with the size of the female, it is concluded that a greater mortality occurs in the larger broods. Incubating fish generally carry some gravel intermingled with the spawn, but it was not clear whether this bore any relation to the survival of the embryos.

In the majority of vertebrates there are distinct qualitative differences between the patterns of reproductive behavior of the male and female. While both sexes have the neuromuscular mechanism capable of eliciting both the male and female patterns, bisexual or homosexual behavior is limited and generally appears under special conditions. *Tilapia* are exceptional in this respect insofar as there are no distinct qualitative differences between male and female in their sexual activities. However, there are marked quantitative differences in all of the patterns.

Several previous investigators have analyzed cichlid mating behavior in terms of Lorenz's releaser concept. It is felt that even in the expanded and modified form presented by Tinbergen, this concept is still too restricted to form an adequate basis for the analysis of *Tilapia* reproductive behavior.

Bibliography.

Anon.

1948. A new Tilapia. *The Aquarium*, 17 (10): 223-226.

Arnold, Joh. Paul and Ernest Ahl

1936. Fremdländische Süsswasserfische. Braunschweig, Germany: Gustav Wenzel und Sohn: 592 pp.

Aronson, Lester R.

1943. The sexual behavior of Anura. IV. Oviposition in the mink frog, *Rana septentrionalis* Baird. *Amer. Mid. Nat.*, 29 (1): 242-244.

1943a. The sexual behavior of Anura. 5. Oviposition in the green frog, *Rana clamitans*, and the bull frog, *Rana catesbeiana*. *Amer. Mus. Nov.*, (1224): 1-6.

1944. The sexual behavior of Anura. 6. The mating pattern of *Bufo americanus*, *Bufo fowleri*, and *Bufo terrestris*. *Amer. Mus. Nov.*, (1250): 1-15.

1945. Influence of the stimuli provided by the male cichlid fish, *Tilapia macrocephala* on the spawning frequency of the female. *Physiol. Zool.*, 18 (4): 403-415.

Asch, Paul

1939. Interessante Beobachtungen an Maulbrütern. *Wochenschr. f. Aquar.-und Terr.-Kunde*, 36 (4): 54.

Bade, E.

1923 Das Süsswasser-Aquarium. Berlin: Fritz Pfenningstorff: 1023 pp.

Beach, Frank A.

1938. Sex reversals in the mating pattern of the rat. *J. Genetic Psych.*, 53: 329-334.

1941. Female mating behavior shown by male rats after administration of testosterone propionate. *Endocrinology*, 29 (3): 409-412.

1942. Analysis of factors involved in the arousal, maintenance and manifestation of sexual excitement in male animals. *Psychosom. Med.*, 4 (2): 173-198.

1945. Bisexual mating behavior in the male rat: effects of castration and hormone administration. *Physiol. Zool.*, 18 (4): 390-402.

1947. A review of physiological and psychological studies of sexual behavior in mammals. *Physiol. Rev.*, 27 (2): 240-307.

Beach, Frank A. and Rasquin, Priscilla

1942. Masculine copulatory behavior in intact and castrated female rats. *Endocrinology*, 31 (4): 393-409.

Bertram, C.K.R., Borley, H. J. H. and Trewavas, E.

1942. Report on the fish and fisheries of Lake Nyasa. London: Crown Agents for the Colonies: 181 pp.

Bodenheimer, F. S.

1927. Zooligische Beobachtungen aus Palistina. I Über die Geschlechterfrage bei maulbrütenden Cichliden. *Zool. Anz.*, 73: 88-93.

BOULENGER, CHARLES L.

1908. On the breeding-habits of a cichlid fish (*Tilapia nilotica*). *Proc. Zool. Soc. London*, 1908: 405-407.

BOULENGER, G. A.

1899. A revision of the African and Syrian fishes of the family *Cichlidae*. Part II. *Proc. Zool. Soc. London*, Part I, 1899: 98-143.

1901. Les poissons du bassin du Congo. Bruxelles: Pub. de l'État Indépendant du Congo: 532 pp.

1906. Descriptions of new fishes discovered by Mr. E. Degen in Lake Victoria. *Ann. & Mag. Nat. Hist.*, 7 Ser., 17 (101): 433-452.

1911. On a collection of fishes from the Lake Ngami Basin, Bechuanaland. *Trans. Zool. Soc. London*, Part 5, 18 (1): 399-430.

1915. Catalogue of the fresh-water fishes of Africa. Vol 3. London: British Mus. (Nat. Hist.): 526 pp.

BREDER, CHARLES M.

1933. On the genesis of oral incubation in fish. *Anat. Rec.*, 57 (4) supplement: 62.

1934. An experimental study of the reproductive habits and life history of the Cichlid fish *Aequidens latifrons* (Steindachner). *Zoologica*, 18 (1): 1-42.

1943. The eggs of *Bathygobius soporator* (Cuvier and Valenciennes) with a discussion of other non-spherical teleost eggs. *Bull. Bingham Ocean. Coll.*, 8 (3): 1-49 + 6 pl.

CARPENTER, C. R.

1933. Psychobiological studies of social behavior in Aves. I. The effect of complete and incomplete gonadectomy on the primary sexual activity of the male pigeon. *J. Comp. Psych.*, 16 (1): 25-97.

DICE, L. R. and LERAAS, H. J.

1936. A graphic method for comparing several sets of measurements. *Cont. Lab. Vert. Genetics, Univ. Michigan*, (3): 1-3.

DIETZ, ADOLF

1926. *Tilapia natalensis* M. Weber. *Wochenschr. f. Aquar.-und Terr.-Kunde*, 23: 433-435.

HEMMINGSEN, AXEL M.

1933. Studies on the oestrous-producing hormone (oestrin). *Skan. Arch. f. Physiol.*, 65: 97-250, 33 text fig.

HEY, D.

1945. Fish keeping in ponds and aquaria. Cape Prov. Admin., Inland Fisheries Dept., Stellenbosch: 50 pp.

1947. The culture of freshwater fish in South Africa. Inland Fisheries Dept., Prov. Admin. Cape of Good Hope: 124 pp.

HOWARD, H. ELIOT

1929. An introduction to the study of bird behaviour. Cambridge Univ. Press, Cambridge, England: 136 pp.

HUXLEY, JULIAN S.

1914. The courtship-habits of the great crested Grebe (*Podiceps cristatus*); with an addition to the theory of sexual selection. *Proc. Zool. Soc. London*, 11: 491-562 + 2 pl.

1938. Darwin's theory of sexual selection and the data subsumed by it in the light of recent research. *Amer. Nat.*, 72 (742): 416-433.

INNES, WILLIAM T.

1944. Exotic aquarium fishes. Innes Publishing Co., Philadelphia, Pa.: 499 pp.

IRVINE, F. R.

1947. The fishes and fisheries of the Gold Coast. The Crown Agents for the Colonies, London: 352 pp.

JUNGHANS, WOLFRAM

1918. *Tilapia microcephala* (Afrikanischer Maulbrüter). *Blat. f. Aquar.-und Terr.-Kunde*, 29:123-125.

LACK, DAVID

1940. The releaser concept in bird behaviour. *Nature*, 145: 107.

LASHLEY, K. S.

1938. Experimental analysis of instinctive behavior. *Psych. Rev.*, 45 (6): 445-471.

LIEBMAN, E.

1933. Some observations on the breeding habits of Palestine cichlidae. *Proc. Zool. Soc. London*, 2 (4): 885-888.

LOCKE, FRANK

1932. *Tilapia microcephala*. *Aquariana*, 1 (2): 34-37.

LONG, JOSEPH A. and EVANS, HERBERT MCLEAN

1922. The oestrous cycle in the rat and its associated phenomena. *Mem. Univ. Calif.*, 6: 1-148.

LORENZ, KONRAD

1935. Der Kumpan in der Umvelt des Vogels. Der Artgenosse als ausloesendes Moment Soziales Verhaltungsweisen. *J. f. Ornith.*, 83 (2): 137-213.

1937. The companion in the bird's world. *The Auk*, 54 (3): 245-273.

LORTET, L.

1875. Sur un poisson du lac de Tibériade, le *Chromis Paterfamilias*, qui incube ses oeufs dans la cavité buccale. *C. R. Acad. Sci., Paris*, 81:2. Semestre: 1196-1198.

1883. Poissons et reptiles du lac de Tibériadae. *Arch. Mus. Hist. Nat. de Lyon*, 3: 99-180.

MARSHALL, F. H. A.

1936. Sexual periodicity and the causes which determine it. *Phil. Trans. Roy. Soc. London*, Ser. B, 226: 421-456.

MYERS, G. S.

1939. A possible method of evolution of oral brooding habits in cichlid fishes. *Stanford Ichthyol. Bull.*, 1: 85-87.

NOBLE, G. KINGSLEY and ARONSON, LESTER R.
1942. The sexual behavior of Anura. 1. The normal mating pattern of *Rana pipiens*. *Bull. Amer. Mus. Nat. Hist.*, 80 (5): 127-142.

NOBLE, G. K. and CURTIS, BRIAN
1939. The social behavior of the jewel fish, *Hemichromis bimaculatus* Gill. *Bull. Amer. Mus. Nat. Hist.*, 76 (1): 1-46.

PEARSON, KARL
1914. Tables for statisticians and biometricians. Univ. Press Cambridge: 143 pp.

PELLEGRIN, JACQUES
1903. Contribution à l'étude anatomique, biologique et taxonomique des poissons de la famille des cichlidés. *Mem. Soc. Zool. France*, 16: 41-400.
1905. L'incubation buccale chez le *Tilapia galilaea* Artédi. C. R. 6th Cong. Int. Zool., 330-332.
1906. L'incubation buccale chez deux Tilapia de l'ogôoué. C. R. 35 Sess. Assoc. Franc. Advan. Sci., 1st Part: 127-128.

PETERS, HANS
1937. Experimentelle Untersuchungen über die Brutpflege von *Haplochromis multicolor*, einem Maulbrütenden Knochenfisch. *Zeitschr. f. Tierpsychol.*, 1 (1): 201-218.
1937a. Untersuchungen über die Brutpflege Maulbrütender Cichliden. *Wochenschr. f. Aquar.- und Terr.-Kunde*, 34 (35/36): 505-510.
1939. Bemerkungen über die Maulbrutpflege. *Wochenschr. f. Aquar. und Terr.-Kunde*, 36 (9): 129-130.
1941. Fortpflanzungsbiologische und Tiersoziologische Studien an Fishen. I. *Hemichromis bimaculatus* Gill. *Zeitschr. f. Morph. und Ökol. Tiere*, 37 (3): 387-425.

RAND, A. L.
1941. Lorenz's objective method of interpreting bird behavior. *The Auk*, 58 (2): 289-291.

ROLOFF, E.
1937. *Tilapia mossambica* Peters. *Blät. f. Aquar.- und Terr.-Kunde*, 48 (4): 80-81.
1938. Die Pflege und Zucht von *Tilapia guinasana* Trewavas 1936. *Wochenschr. f. Aquar.- und Terr.-Kunde*, 35 (32): 501-502.
1939. *Tilapia guinasana* Trewavas 1936, dunkle Abart. *Wochenschr. f. Aquar.- und Terr.-Kunde*, 36 (41): 617-619.

SCHNEIRLA, T. C.
1941. Social organization in insects, as related to individual function. *Psych. Rev.*, 48 (6): 465-486.
1946. Problems in the biopsychology of social organization. *J. Abnormal and Social Psych.*, 41 (4): 385-402.

SCHOENFELD, MILTON
1934. Anomalies and Oddities. *Home Aquar. Bull.*, 4 (2): 14; 18-19.

SCHREITMÜLLER, W.
1920. *Tilapia microcephala* (Kleinköpfige Tilapia) und ihre Zucht im Aquarium. *Blät. f. Aquar.- und Terr.-Kunde*, 31 (14): 209-211.
1936. Ein neuer Maulbrüter. *Das Aquarium*, 10: 66-67.

SEITZ, ALFRED
1940. Die Paarbildung bei einigen Cichliden. I. Die Paarbildung bei *Astatotilapia strigigena* Pfeffer. *Zeitschr. Tierpsych.*, 4 (1): 40-84.
1942. Die Paarbildung bei einigen Cichliden. II. Die Paarbildung bei *Hemichromis bimaculatus* Gill. *Zeitschr. Tierpsych.*, 5 (1): 74-101.

SELEUTHNER, J.
1941. *Tilapia mossambica* Peters. *Wochenschr. f. Aquar.- und Terr.-Kunde*, 38 (37): 362-363.

SIMPSON, GEORGE GAYLORD and ROE, ANNE
1939. Quantitative Zoology. McGraw-Hill Book Company, Inc., New York: 414 pp.

SNEDECOR, GEORGE W.
1946. Statistical Methods. The Collegiate Press, Inc., Ames, Iowa: 485 pp.

STOYE, F. H.
1935. Tropical Fishes for the Home. Carl Mertens, New York: 284 pp.

SVENSSON, GUSTAV S. O.
1933. Fresh water fishes from the Gambia River (British West Africa). *Kungl. Sv. Vet. Akad. Handl.*, 12 (3), Series 3: 1-102.

TINBERGEN, N.
1939. On the analysis of social organization among vertebrates, with special reference to birds. *Amer. Midland Nat.*, 21 (1): 210-233.
1948. Social releasers and the experimental method required for their study. *Wilson Bull.*, 60 (1): 6-51.

TREWAVAS, ETHELWYNN
1942. The cichlid fishes of Syria and Palestine. *Ann. & Mag. Nat. Hist.*, 11 Series, 9 (55): 526-536.

WHITMAN, C. O.
1919. The behavior of pigeons. (Posthumous works of Chas. Otis Whitman, Vol. III). Carnegie Inst. of Wash.: 161 pp.

EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. Male cleaning nest. × .5

Fig. 2. Oviposition. The male is behind the female, waiting for her to move along so that he can pass over and fertilize the eggs. × .5

Plate II.

Fig. 3. The male is fertilizing the eggs while the female is circling the nest. By the time fertilization was completed the female was directly behind the male, ready to lay a second round of eggs. × .5

Fig. 4. Male picking up the eggs. All of the eggs were gathered up in less than one minute. × .5

Plate III.

Fig. 5. Male carrying eggs. × .7
(Photo. by S. C. Dunton, N. Y. Zool. Soc.).

Fig. 6. In special circumstances the female may carry the spawn. An egg can be seen at the tip of the open mouth of the female. × .5

Addendum.

When this report was in page proof an article by Alfred Seitz (1948)—Vergleichende Verhaltensstudien an Buntbarschen (Cichlidae).—Zeitschrift für Tierpsychologie, *6* (22): 202-235, was received from Germany. Here Seitz analyzes fighting and courtship behavior in two cichlid species, *Tilapia heudeloti* and *Tilapia natalensis*, in accordance with the theory of instinctive movements of Konrad Lorenz. On page 134 of the present paper we have noted the very close similarities of *T. heudeloti* and *T. macrocephala;* they may in fact be varieties or subspecies. However, the pictures of *T. heudeloti* presented by Seitz, the descriptions of the external morphology, particularly coloration, as well as the descriptions of courtship and fighting behavior, all suggest that he was dealing with a very different fish. It is not possible at this time to comment further on Seitz's paper, nor do we wish to venture any opinions concerning the complex problems of cichlid taxonomy, except to suggest to the reader who may wish to compare Seitz's paper with the present report that the *T. heudeloti* of Seitz and our *T. macrocephala* are perhaps very different species. —L.R.A.

FIG. 1.

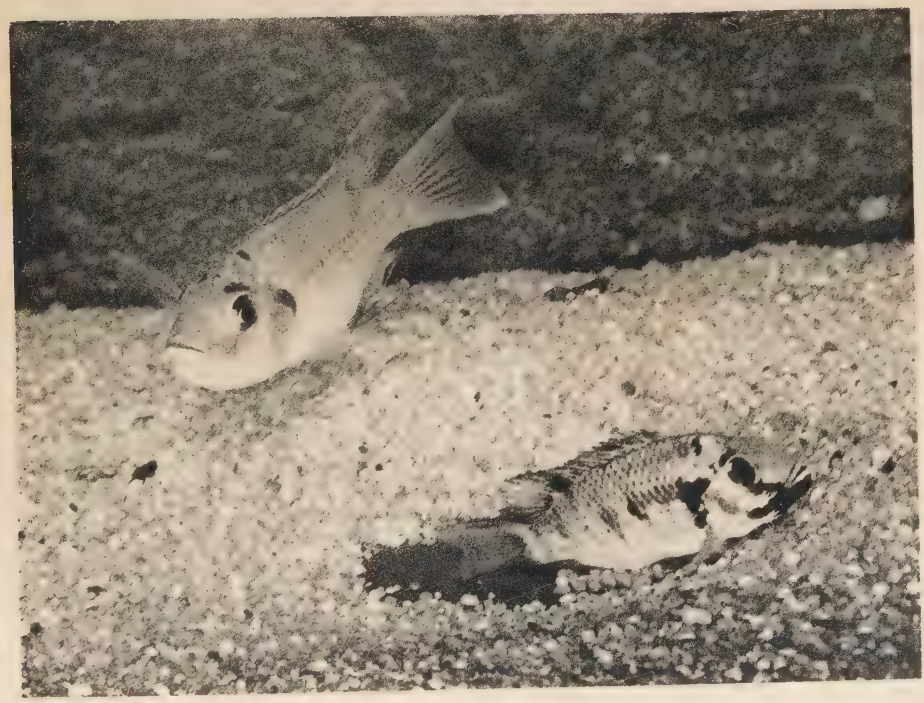


FIG. 2.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE MOUTHBREEDING CICHLID FISH, TILAPIA MACROCEPHALA (BLEEKER).

FIG. 3.

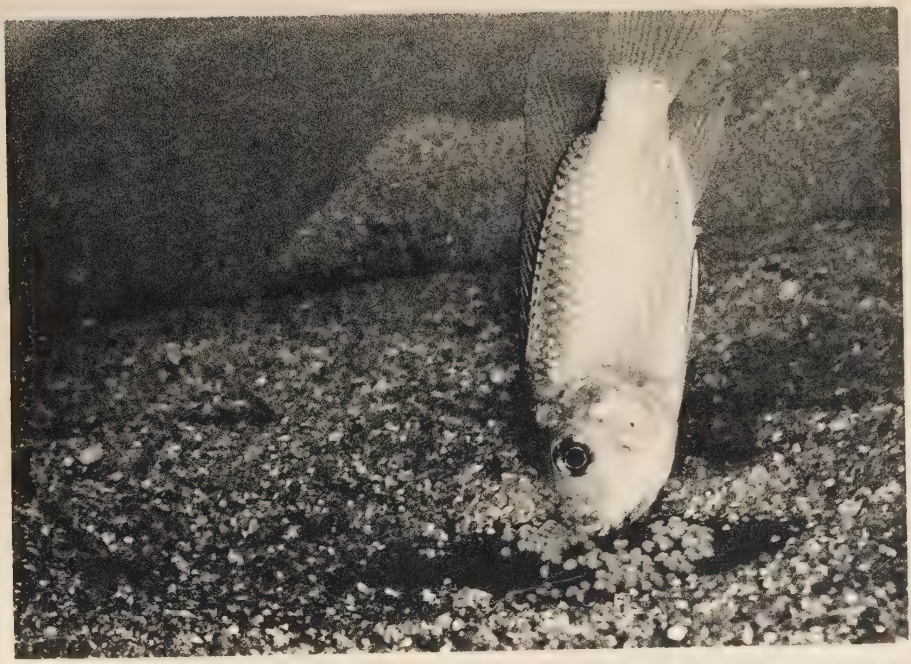


FIG. 4.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE MOUTHBREEDING CICHLID FISH, TILAPIA MACROCEPHALA (BLEEKER).

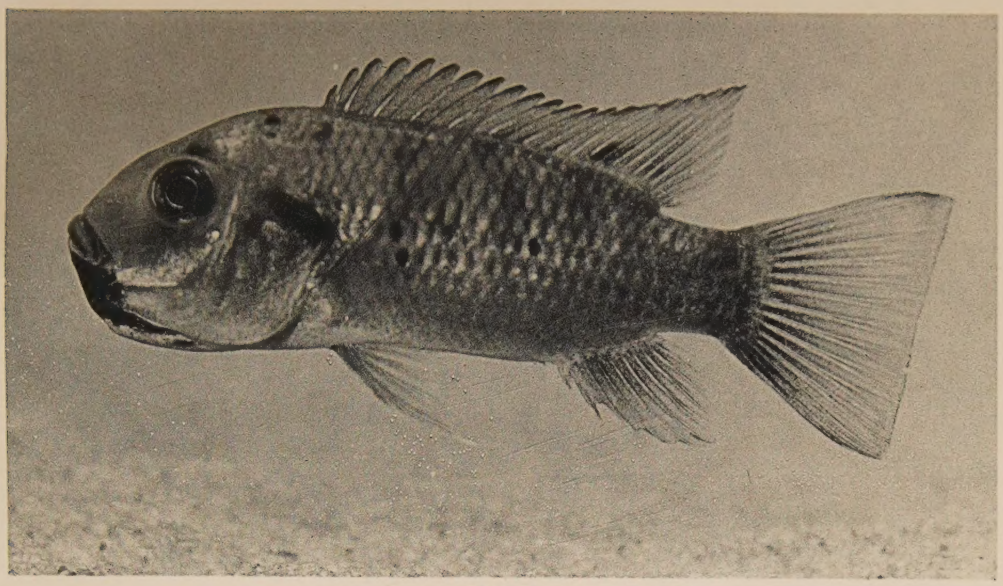


FIG. 5.

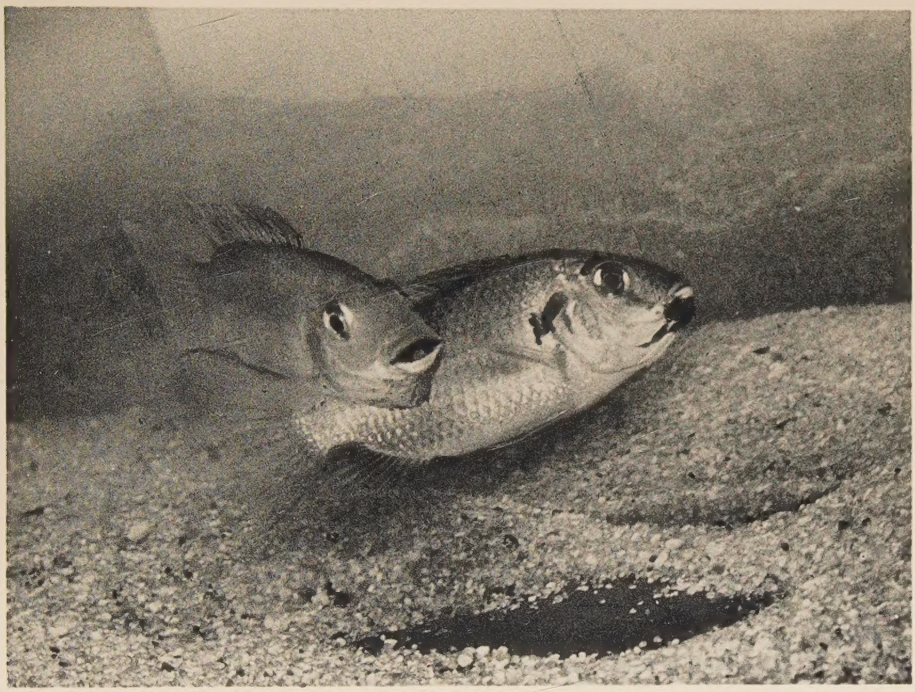


FIG. 6.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE MOUTHBREEDING CICHLID FISH, TILAPIA MACROCEPHALA (BLEEKER).

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